

















XXIV. Researches on the Structure, Physiology, and Development of Antedon (Comatula, Lamk.) rosaceus.—Part I. By William B. Carpenter, M.D., F.R.S.

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#### I.—INTRODUCTION.

That the only secure basis of Zoological Science is afforded by a thorough elucidation of the structure and life-history of typical forms representing particular subdivisions of the Animal Kingdom, will not, I anticipate, be disputed by any Naturalist of the present day. And every one who is even slightly acquainted with the history of that Science must be well aware that the standard Monographs which have been devoted to this object have exerted a more permanent influence on its progress, than have any of those comprehensive Systems which have been set up from time to time, and, after lasting for a while, have been overthrown to make way for others scarcely more durable. For any System of Classification is liable to be invalidated by new discovery; and the utmost which can be claimed for it is, that it accurately represents the state of knowledge at the time of its promulgation. But every Monograph which contains a faithful description of the structure and life-history of any type whatever, however far it may be from absolute completeness, presents a body of facts which subsequent research may add to but cannot set aside; and may come to acquire, even at a long subsequent period, a value not anticipated by its author.

I cannot suppose, therefore, that any apology is needed for my offering to the Royal Society a detailed account of perhaps the most interesting of our British Echinoderms; of which the structure, notwithstanding the attention given to it by various eminent Anatomists, has been hitherto but very imperfectly made out; whilst of its life-history still less is known. That I have solved every problem which its study has presented, is far more than I can affirm; but I venture to think that what I now bring forward will stand the test of future scrutiny; and that the results I have attained will prove of importance, not merely in leading to a better understanding of the important group of which Antedon is a representative, but also in helping to the solution of certain fundamental questions in General Physiology.

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The peculiar interest of Antedon as a "typical form" arises from its being the only representative now left in British seas of that wonderful Order Crinoïdea, which, under various modifications, has maintained its place in our Fauna from the Silurian epoch to the latest Tertiary period. It is true that in some important particulars, Antedon is a less characteristic representative of the Crinoïdea than is the existing Pentacrinus of the West Indian seas; and a complete Monograph of the structure and life-history of that organism would be one of the most valuable contributions which Palæo-zoological science could receive. But for such a Monograph there is unfortunately no reasonable ground of hope. The rarity with which specimens of this Pentacrinus have occurred, and the imperfection of the state in which they have been preserved, have hitherto prevented any save a very unsatisfactory account of its structure from being given; although the best of these specimens fell under the examination of an Anatomist and Physiologist no less able than Professor Johann Müller. And even supposing that a fortunate chance should throw a perfect and well-preserved specimen in the way of some equally accomplished Naturalist, he could do no more than give a minute description of its organization; -a knowledge of its life-history being likely to remain unattainable, on account both of the rarity of the species and of the great depths at which alone it is found.

Moreover, although in its adult state Antedon seems to depart widely from the typical Crinoids, in having neither root nor stem, and in possessing a power of free locomotion of which they are altogether destitute, yet this departure involves what is really (in a physiological point of view) the least essential part of the Crinoidal fabric;—a part, moreover, which exists in that earlier stage of this animal's life, wherein it is in this as in all other particulars a true Crinoid; and which is afterwards replaced, so far as its function is concerned, by a prehensile apparatus that is subservient to the very same purpose. For, as I shall show hereafter, the mature Antedon habitually clings by its dorsal cirrhi to a fixed attachment, so as to resemble its Pentacrinoid larva in its ordinary habit; using its power of free locomotion only when persistence in its position would be no longer conformable to its requirements.

It has been, therefore, because every addition to our knowledge of Antedon contributes to the elucidation of the structure, physiology, and life-history of the Crinoïdea generally, that I have thought it worth while for some years past to devote a considerable portion of such brief periods of leisure as I have been able to command, to the careful study of the species (A. rosaceus) which presents itself abundantly on various parts of our northern, western, and southern shores. When I commenced this study, I entertained the hope of being able to trace out the whole history of its development, from the very commencement of its existence as a free-swimming larva. But I soon found that the earlier stages of this process take place during a part of the year in which my official duties do not allow of my visiting the coast; and learning that Professor Wyville Thomson was able and willing to undertake this part of the inquiry, I gladly arranged with him that he should work out the developmental history of Antedon as far as the

early Crinoidal stage, from which I should myself be prepared to take it up; and thus his Memoir on the Embryology of *Antedon rosacens*, which has already appeared in the Philosophical Transactions (1865), will serve as the complement of my own.

Before proceeding, however, to detail the results of my researches, I think it right to give a somewhat particular account of what has been already done by those who have made a special study of Antedon; and also to mark out the principal stages in the progress of our general knowledge, both of the true character of the Crinoïdea as constituting one of the primary Ordinal subdivisions of the Class Echinodermata, and of the relationship of the typical Crinoids to Antedon. It will appear in this Historical Summary (p. 682) why I have thought it right, in concurrence with the views of Dr. J. E. Gray, Professor Wyville Thomson, and the Rev. Alfred M. Norman, to revert to the generic name Antedon given to this type by Freminville, in preference to using either the designation Comatula conferred upon it by Leach, which is used by the Scandinavian Naturalists.

#### II.—HISTORICAL SUMMARY.

The earliest account of Antedon which I have been able to find, occurs in the 'Phytobasanus'4 of Fabius Columna; an author who deserves to be commemorated for the excellence of his descriptions of various plants and animals, and for the fidelity and beauty of his delineations, which were engraved on copper and printed on the same page with the letter press. The figure he gives of his δεκαδασυακτινοειδής is so characteristic as to enable me almost certainly to identify it with the species which forms the subject of the present memoir; indeed I do not think it has been since surpassed by any figure not drawn from the animal in its natural position during life. I quote the words in which this author commences his description, as indicating the remarkable abundance of the specimens that fell under his notice, and the strong impression made upon him by their beauty:—"Nova et perelegans est hujus Stellæ forma, ab aliis omnibus differens nec adhuc descripta, nostro litori frequens, ita ut nec ulla retrahantur retia, quin ipsis implicata, et simul cum piscibus in foro etiam non inveniatur." He gives a very accurate description of its jointed arms and of its dorsal cirrhi; but he fancied that the latter were used to grasp food and to draw it into the mouth, which he erroneously supposed to be at the central point from which they radiate. Of the soft visceral mass occupying the ventral cavity of the cup, and having the mouth in its centre, he says, "ex adversâ parte corpus conspicitur rotundum, læve, molle, cujus interiora propter tenuitatem con-

<sup>&</sup>lt;sup>1</sup> British Museum Catalogue of British Radiata, p. 28.

<sup>2</sup> Op. cit.

<sup>&</sup>lt;sup>3</sup> "On the Genera and Species of British Echinodermata," in Annals of Natural History, 3rd ser. vol. xv. p. 99 (Feb. 1865).

<sup>&</sup>lt;sup>4</sup> Φυτοβάσανος, sive Plantarum aliquot Historia. Neapoli, 1592.

<sup>&</sup>lt;sup>5</sup> See p. 12 of the Appendix to the Phytobasanus, entitled "Piscium aliquot Plantarumque novarum Historia."

siderare nequivi; ipsum verò et facillimè disjungitur a stellà." Its colour he originally speaks of as subrubens; but in a later treatise¹ (Observationes, Cap. III. p. 5) he describes it as croceum; and he further remarks,—"reperiuntur frequenter vario colore distinctæ veluti maculosæ; partes quidem cirrorum lutescentes, aliæ albicantes, aliæ rubentes, aliæ pullo colore,"—a variety which has continually fallen under my own observation. And he further notes the remarkable fact that if these animals are placed whilst yet alive in fresh water, they impart their colour to it in a very short time.

The figure and description of Fabius Columna were adopted, without the addition of any further particulars, by Aldrovandus in his great work 'De Animalibus Insectis' (*Bononiæ*, 1602); and from this it seems to have passed into other systematic treatises of the 17th Century.

At the end of that century, however, there occurs a very remarkable notice of this type, on the part of a naturalist who deserves more honour than he has gained; namely EDWARD LLHUYD<sup>2</sup>, who succeeded Dr. Plot as Head Keeper of the Ashmolean Museum.

In order rightly to appreciate its value, we must look back to the history of the ideas which had prevailed up to that time in regard to the fossil Crinoïdea.

The earliest author who systematically treated of Crinoidal remains was the celebrated Agricola<sup>3</sup>; although from the manner in which he speaks of them it is evident that they had long attracted the attention of Naturalists, and that the names Trochites, Entrochus, and Encrinus had found their way into general use,—the first being applied to the separated joints of cylindrical stems, the second to fragments of similar stems composed of several joints, and the third to the summits, especially to that of Encrinus liliiformis, the species most commonly known. Of the real relationship of the three kinds of bodies thus distinguished, he does not seem to have had any idea. Agricola further gave the distinctive designation Pentacrinus to crinoidal summits which had lost their digitations, and which showed five principal radiations; whilst he conferred that of Astroites or Asteria upon fragments of pentagonal stems, of which each separate joint presents some resem-

<sup>&</sup>lt;sup>1</sup> Minus cognitarum rariorumque nostro cœlo orientium stirpium  $\tilde{\epsilon}\kappa\phi\rho\alpha\sigma\iota s$ , . . . item de Aquatilibus aliisque nonnullis Animalibus libellus.  $Rom\alpha$ , 1616.

<sup>&</sup>lt;sup>2</sup> LLHUYD was born in Carmarthenshire in the year 1670; was a student of Jesus College, Oxford; travelled for scientific purposes throughout England, Scotland, Ireland, and Brittany; and died at the early age of thirty-nine. His merits were thoroughly appreciated by the late Professor E. Fordes, who, in dedicating to him the genus Luidia, thus culogizes him:—"He was a man of great knowledge and great talent. His studies were extended over large tracts of science and literature, and he enlightened both with his researches and his writings. He united a comprehensive and philosophical mind with an observing eye, and the energy to execute. Amid the multiplicity of his studies there was no confusion. He wrote on insects, plants, fossils, antiquities, and languages; on all much and well. His principal works were 'Lithophylacii Britannici Ichnographia,' and 'Archæologia Britannica.' Ray praised him. Strange to say, his name is omitted in many of our cyclopædias, which devote whole pages to men of less repute." (British Starfishes, p. 136.)

<sup>&</sup>lt;sup>3</sup> See especially Book V. of the Supplement "De Naturâ Fossilium" to his great work 'De Re Metallicâ,' first published about 1530, and many times subsequently reprinted.

blance to a Starfish. The descriptions of Agricola were repeated by Conrad General, who gave a figure of a portion of the stem of Pentacrinus briareus under the name of Asteria, and of a portion of the stem of Enerinus liliiformis under that of Entrochus; like his predecessor, moreover, approximating the Crinoids to the "lapides judei" (fossil spines of Echini) and to Belemnites. No advance seems to have been made in the knowledge of the Crinoïdea until 1669, when Lachmund's for the first time figured a complete specimen of Encrinus liliiformis under the name Pentagonos, and showed that the Entrochi and Trochites were really parts of the same organism. Better figures of the summits of some palæozoic Crinoïdea were soon afterwards given by Martin Lister in his "Description of certain stones figured like plants, and by some observing men esteemed to be plants petrified"3: but having unfortunately adopted the erroneous notion that the Crinoids were the fossil remains of Plants which had lived at a great depth in the sea, he was led to regard the body of the Crinoid as the base of the stem, and its arms as ramifications of the roots. Two years afterwards Lister published figures of some stems of Pentacrinus<sup>4</sup>, which also he regarded as representing marine plants. And not long subsequently he was followed by Beaumonts, who described and figured some additional types of palæozoic Crinoïdea under the name of "rock-plants growing in the lead mines of Mendip Hills."

It was under the influence of such misconceptions on the part of the best-informed Naturalists of the time,—as well as of the doctrine still prevalent among the less instructed, that fossils are nothing else than "curiously figured stones" deriving their peculiar shapes from some "plastic virtue latent in the earth,"—that the researches of Llhuyd upon the fossil Crinoïdea were commenced; and it is therefore very much to his credit that he should have made such an important step in advance, as not only to refer these remains to the same group with the Sea-stars, but also to fix upon that particular Sea-star which we now know under the name Antedon, as the type to which they are most nearly allied. As this fact has been entirely ignored by the recent historians of this department of Palæontology, MM. DE KONINCK and LE HON<sup>6</sup> (to whose labours I

- <sup>1</sup> De Rerum Fossilium, lapidum et gemmarum maxime, figuris et similitudinibus liber. *Tiquri*, 1565.
- <sup>2</sup> Oryetographia Hildesheimeusis, pages 58, 59.

  <sup>3</sup> Philosophical Transactions, No. 100 (1673).
- 4 "A letter containing his observations of the Astroïtes or Star-Stones," in Philosophical Transactions, No. 112 (1675).
  - <sup>5</sup> Philosophical Transactions, No. 129 (1682), and No. 150 (1683).
- 6 Recherches sur les Crinoïdes du Terrain Carbonifère de la Belgique. Bruvelles, 1854.—The following is all the mention made by these authors of the researches of Linuyd. "A la fin du XVII<sup>me</sup> siècle parut l'ouvrage de Lwyd, qui, par les nombreuses figures qu'il contient et les changements que son auteur fit subir à la nomenclature de son époque, semble avoir produit une assez vive impression dans le monde savant au moment de sa publication. L'auteur y a employé divers noms pour désigner les différens fragmens de Crinoïdes qu'il a figurés, ou qui ont fait partie de sa collection. C'est ainsi qu'il donne les noms génériques de Porpites, d'Entrochus, de Volvola, et d'Asteria à des fragmens de tiges de divers espèces de Crinoïdes; qu'il désigne sous celui de Stellaria, de Volvola, de Modiolus, et d'Astropodium un certain nombre de sommets et de fragments de sommets de ces animaux. Ce dernier nom suffit pour faire comprendre que Lwyd, à l'exemple de Lister et de Braumont, a confendu ces sommets avec leurs racines" (p. 30).

am indebted for several references to the authors named in this summary), I think it right to cite the evidence of it in some detail.

The 'Lithophylacii Britannici Ichnographia' of Edward Llhuyd' (1699) is a work which, the more it is examined, leaves a stronger and yet stronger impression of the industry and sagacity of its author. To elucidate the nature of Fossils by the comparison of their forms with those of existing Animals and Plants,—familiar as the principle now seems to us.—had not been systematically attempted (so far as I am aware) by any previous Naturalist; and no one who may bestow a little attention on the contents of the 'Lithophylacium' can fail to perceive that it is something much more valuable than a mere collector's catalogue, and deals with questions far more important than those of nomenclature. LLHUYD's sixth class, that of Crustacea punctulata, includes all the fossil remains which we should now refer to the Class ECHINODERMATA; and in the general observations at the head of this division he expressly says,—"unde ad hanc classem retulimus omnes lapides ejusmodi materià conflatos; sive ii ad Echinos spectent, ... sive ad Stellas marinas, ut Astrorrhiza, Astropodium, Asteria, Entrochus, Volvola, Appendicula, &c." (these being the names which he assigned to various Crinoïdal fragments). Further, in the supplemental Epistolæ contained in the same volume, we find an express discussion on the relations of the Encrinus of LACHMUND, the Entrochus of Agricola, and the Asteria of Plot, to existing forms of Sea-stars, as well as of the separated parts just named to each other; and it is quite obvious that he was perfectly satisfied that these fossils were neither minerals nor plants, but stony ossicles of Sea-stars. He not only put forth this conviction with yet greater earnestness in a subsequent Memoir<sup>2</sup>, which seems to have escaped the notice of the historians just cited, but even distinguished Antedon as the particular Sea-star to which the Crinoïdea are most nearly related. His statements on this point are so remarkable as to deserve being quoted in

The dedication of this work to Martin Lister is in the following terms, alike honourable to both parties:

—"Erudito imprimis viro D. Martino Lister, Doctori Medico scriptis et praxi claro, Societatis Regiæ Socio illustrissimo; Musei Oxoniensis, post ipsum cujus nomen præfert nobilissimum Ashmolum, fautori primario; Bibliotheeæ ibidem physicæ et antiquariæ fundatori munifico; fossilium Britanniæ insulæ indagatori primo et fælici; præceptori suo indulgentissimo et Mecænatiæternum colendo; hane qualemeunque Lithophylacii Britannici Ichnographiam, officii et gratitudinis ergo, humillime offert ac dedicat Edvardus Luidius."—Of the esteem in which the labours of Luidun were held by his contemporaries, a very interesting record is contained in the following notification:—

Huius Libri centum et viginti tantum Evemplaria impressa sunt, impensis infrascriptorum

## ILLUSTRISS. VIRORUM,

- D. Baronis Sommers, summi Angliæ Cancellarii.
- D. Comitis de Dorset, &c.
- D. C. Montague, Cancellarii Scaccarii.
- D. Isaaci Newton.
- D. M. Lister.

- D. T. Robinson.
- D. H. Sloan.
- D. Fr. Aston.
- D. Geoffray, Parisiensis.

<sup>&</sup>lt;sup>2</sup> 'Prælectio de Stellis Marinis Oceani Britannici, nec non de Asteriarum, Entrochorum, et Enerinorum Origine,' published at Oxford in 1703, and incorporated as an Appendix in the great work of Linckius, 'De Stellis Marinis' (1733), and also in an edition of the 'Lithophylacium' published in 1760.

his own words. After describing nine specimens of different kinds of recent Starfish. he proceeds (§ XVIII.) as follows:-"Inter has decem, tum ob elegantiam, tum quod maxime rara sit, primas tenet, quæ decimo loco exhibetur, decempeda Cornubiensium; seu Stella rubra loricata, claviculato modiolo; quinis radiis constans, pennatis ab exortu bifidis. In Cornubia juxta Pensans cum antecedente reperimus, sed longinguo maris refluxu. A Stella decem radiorum Columnæ, si diversa sit, parvitate præsertim distinguenda est. Columna enim suæ Stellæ pedalem tribuit longitudinem, cum nostra sex aut septem uncias non exsuperet." With this Decempeda Cornubiensium, the Stella Δεκάκνημος rosacea of Linck, our own Antedon rosaceus, Lliuyd afterwards (δ xxx.) compares a fossil "e fodinis Glocestrensibus," and specifies the following as the points of similarity:—"Videmus enim (1), modiolum esse utrique; (2) modiolo appendentes claviculas aut capreolos; (3) quinos radios, a primo exortu bifidos; (4) articulorum cujuslibet radii commissuram loricatam; (5) denique, radiis ab inferiori parte articulatim adnascentes aristas. Hisce visis, Stellam decempedam lapideam, aut fossilem, hunc lapidem pronunciare, nemo, opinor, dubitabit. (§ xxxI.) Fatemur nihilominus, quoad modiolorum figuram, multum interesse discriminis, cum lapidea Stella quasi ansellam habeat stellatam, ubi altera scutulum; et hanc majoris esse molis marinâ. Verum hæ notæ aliam tantum speciem inferunt, genus non tollunt. Concesso itaque, hunc lapidem decempedam esse; comperimus tandem Asteriam nonnullam nihil aliud fore, quam decempedæ modiolum; quod ex hoc ipso specimine manifestum est. Dixi nonnullam, quoniam variæ dantur Asteriæ, earumque aliquot Stellarum, quas coriaceas diximus, vertebras exprimere alias docuimus, et ex No. 19, ubi Asteriæ parvæ cum Asterisci ossiculis denudatis conferuntur, propemodum constare arbitror." In the same method of careful and intelligent comparison he proceeds in subsequent sections to show that the Encrinus of Lachmundus is similarly related to his Decempeda; and although he seems to have been far from comprehending the true character of the stems of the Crinoïdea (no recent pedunculate type of the group having been known to him), vet I think that no one who peruses the passages I have quoted can refuse him the credit of having-not as a mere guess, but on the sound basis of anatomical correspondencedistinctly predicated the intimate relationship between our recent Antedon and the fossil CRINOIDEA; a relationship that was subsequently overlooked by Zoologists of the highest eminence, and has only within a comparatively recent period come to be generally admitted.

The credit of having explicitly pointed out that the Crinoïdea, far from belonging to the Vegetable kingdom, are true Animals, closely approximating in structure to the existing types known as "Sea-stars," is assigned by MM. Koninck and Le Hon, as also by MM. Blainville and Dujardin, to Rosinus. Not only, however, was his treatise on the subject posterior by sixteen years to that of Llhuyd, but his conclusion was much less exact; his approximation of the Crinoïdea having been not to the genus

<sup>&</sup>lt;sup>1</sup> 'Tentaminis de lithozois ac lithophytis olim marinis, jam vero subterrancis, prodromus, sive de stellis marinis quondam, nunc fossilibus disquisitio.' *Hamburgh*, 1719.

Antedon but to the genus Euryale. Hence it is obvious that in regard alike to LLHUYD'S priority in time, and to the greater accuracy of his conclusion, we are justified in claiming for our own countryman the merit of having been the first to take up this important position.

Returning now to the history of Antedon, we find it characteristically described as a peculiar type of "Sea-stars" in the remarkable work of Linckius1; who seems to have been the first to attempt to bring together the large number of forms of this group acquired by the industry of collectors, and to endeavour to systematize them. Although his principles of classification were far from sound, and conducted him to an arrangement which was in many respects erroneous, yet they led him to erect Antedon (of which six species regarded by him as distinct are described under three generic names) into a group distinct not only from the Asteriadæ, but also from the Ophiuridæ, with which they have been associated by many later systematists. To this group (termed by him a Class, but rather in reality a Family) he assigned the name Crinitæ sive Comatæ Stellæ, on account of the hairy appearance given to the arms by the "capillary fibres" with which they are fringed; thus distinctly foreshadowing the name Comatula conferred upon this generic type by Lamarck. The first of his genera he named Δεκάκνημος, to indicate its possession of ten radiating cauda crinita; and he ranges under it three species, (1) the Crocea Zaffarana Neapolitanorum, οτ δεκαδασυακτινοειδής of Fabius Columna, (2) the Rosacea or Decempeda Cornubiensium of Llhuyd, and (3) the Barbata or fimbriata of Barrelier. Of the first he quotes Columna's description without copying his figure; of the second he gives a figure, which though imperfect, is sufficient for its identification, and speaks of it as distinguishable from the preceding only by its inferiority of size, Columna's Seastar being often a foot in diameter, whilst the diameter of LLHUYD's does not surpass 6 or 7 inches; of the third also he gives a figure, which shows it to be only another variety of the preceding, at the same time quoting the description given by Barrelier<sup>2</sup>, who partook of the misapprehension of Columna respecting the use of the dorsal cirrhi,

<sup>1</sup> Johannis Herrici Linckii Lipsiensis 'De Stellis Marinis liber singularis. Tabularum Ænearum Figuras exemplis nativis apprime similes et Autoris Observationes disposuit et illustravit Christianus Garriei Fischer Regiomontanus.' Lipsia, 1733.—This work deserves special notice on many accounts. Its author, a Pharmacopolist at Leipzig, was a Foreign Member of the Royal Society, to the President and Fellows of which it is dedicated. The large number of types which are described and admirably figured testify to the industry and zeal of its author as a Collector, who seems to have spared neither pains nor expense in procuring specimens from every quarter of the world; and it is peculiarly interesting to find that a main purpose of the formation of this collection was to throw light on the exact nature of those Fossil remains, whose general resemblance to the Sea-stars was clearly enough recognizable, but whose precise affinities could not be predicated with certainty from anything then known. "In terris per omnem naturalis historiæ memoriam nihil repertum simile; in mari analogiam præ se ferebant viventia aliqua, sub latiore stellarum marinarum genere, ramorum insectorum charactere differentia. Sed nulla hujus generis reperiebatur species, cui quantitas et articulorum configuratio congruebant. Quærendæ stellæ novæ erant, ut instituta cum petrefactis ruderibus collatione, et genus et primæva forma clucerent." (Preface.)—The binomial nomenclature, moreover, is employed more systematically by Linckius, than by any other pre-Linnæan author with whom I am acquainted.

<sup>&</sup>lt;sup>2</sup> Barrelieri, Jacobi, 'Plantæ per Galliam, Hispaniam, et Italiam observatæ.' Paris, 1714.

these being likened in function to the proboscis of the Elephant or the upper lip of the Horse. His second genus, named Τρισκαιδεκάκνημος, is based on a specimen described by Ρετινεκ¹ as having thirteen arms; this specimen, however, he suspects to have been imperfect. To his third genus he gave the designation Caput Medusa, which had been previously applied to the type since known as Euryale; apparently thinking that it might be much more appropriately conferred on Sea-stars having very numerous (sixty or more) straight capillated arms, than on those with ramifying and twining but naked arms, to which he gave the name Astrophyton. Of the Caput Medusæ he described and figured two species, brunneum and cinereum, both from the Museum of Seba; these do not seem to differ, however, in anything but size and colour.

It is not a little remarkable that notwithstanding the correct approximation of the CRINOÏDEA by LLHUYD to the nearest type of the Echinoderm group then known, and the prominence given to his views by their incorporation in the important systematic treatise of Linckius, they should have been almost entirely without influence on the opinions of the most eminent Naturalists of the 18th Century. For, to pass by the notion of one that the stems of Encrinites are parts of the vertebral column of certain Fishes, and the idea of another that they are the products of the siphon of Orthoceratites, we find Ellis<sup>2</sup> (in 1753) suggesting that his Umbellularia Encrinus (the Pennatula Encrinus of Pallas<sup>3</sup>) is the analogue of the Encrinus liliiformis, a figure of which he places by the side of that of his "cluster-polype" for the sake of comparison. He seems, however, to have had his doubts of the reality of this resemblance rather strengthened than removed by further inquiry; for in his 'Essay on Corallines' published two years afterwards, we find him, whilst repeating his previous figures, thus expressing himself:— "At K is a figure of the Encrinos or Lilium Lapideum; which, whether it may not be the petrified Exurine of this Animal, is submitted to the consideration of the curious in Fossils; for they have not yet been able, I apprehend, to fix upon anything more probable. The difference that appears to me, upon consulting Rosinus, a German author, who has published a treatise at Hamburgh particularly on this curious fossil, is that the Encrinos has rather been a species of Starfish, with a jointed stem or tail; and the rays of the star, instead of having Tentacula, or claws, at the end of each, like our Polype, are furnished with ranges of jointed fibres, along the inside of each ray like a brush; of which the same author has given a curious plate, with a particular description of this extraordinary fossil." (Op. cit. p. 99.) The notion of the relationship of Encrinus to Umbellularia and its Zoophytic allies, thus suggested by Ellis, was explicitly adopted by Mylius4 in a treatise which he published at the same period on the same subject;

<sup>&</sup>lt;sup>1</sup> Petiveri, Jacobi, 'Gazophylacium Naturæ et Artis;' Londini, 1711:—also 'Aquatilium Animalium Amboinensium, Icones et nomina;' Londini, 1713.

<sup>&</sup>lt;sup>2</sup> Philosophical Transactions, vol. xlviii. part 1, p. 305.

<sup>&</sup>lt;sup>3</sup> Elenehus Zoophytorum. Hagæ Comitum: p. 365.

<sup>&</sup>lt;sup>4</sup> Beschreibung einer neuen Grönlandischen Thierpflanze, pp. 16, 17. Hannover, 1753, and London, 1754.

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and it seems to have been generally accepted, notwithstanding Ellis's own hesitation, since we shall find it to have been the source of the extraordinary misconception in regard to the nature of the Crinoïdea adopted by one of the most eminent Zoologists of the commencement of the 19th Century, especially distinguished by his knowledge of Invertebrate Animals.

The discovery of a recent specimen of a pedunculated Crinoid, which was announced by Guettard in 1755, did not (as might have been expected) supply the correction of this error; for although he noticed the strong resemblance between this so-called Palmier marin and some of the Starfishes described by Linck, yet being unable to discover a central mouth, he seems to have concluded that this resemblance was fallacious, and to have believed that nourishment was imbibed by the animal through the numerous minute pores which he affirmed to exist at the extremities of the tentacles and pinnules,—thus likening it to the Zoophytic type, although he refrained from ranking it definitely with that group. In his comparison of it with the fossil Crinoïdea he made an extraordinary blunder, which was the reverse of that of Lister; for whilst the latter mistook their summits for radiating and subdividing roots, Guettard imagined that the more or less regularly ramifying roots of Apiocrini were in reality their summits. Another specimen of the recent *Pentacrinus* very shortly afterwards (1761) came under the notice of Ellis2, whose description of it is entitled "An account of an Encrinus or Starfish, with a jointed stem, taken on the coast of Barbadoes, which explains to what kind of animal these fossils belong, called Starstones, Asteriæ, and Astropodea, which have been found in many parts of this kingdom." The specimen examined by him was so imperfect that he did not recognize the place of the mouth; nor did he in any way more distinctly indicate than in the title just quoted the relationship of this organism to the Starfishes. Not having the base of the stem, he felt himself unable to affirm whether it moved freely through the sea, or was attached to the bottom like Corals and Sponges; and it is only by inference that it can be concluded that he was led by the study of this specimen to abandon his previous notion of the relationship of the Crr-NOÏDEA to "cluster polypes."

It was unfortunate for science that Linneus, instead of adopting the more advanced views of some of his predecessors as to the true relations of the Crinoïdea, was so misled by the jointed structure of their stems as to rank them among Zoophytes in the genus *Isis*; whilst he threw back *Antedon* among the other Starfish, ranking them all together in his genus *Asterias*<sup>3</sup>. And this arrangement was left unaltered in the twelfth edition of his 'Systema Naturae' published in 1766, notwithstanding the appearance of the

<sup>&</sup>lt;sup>1</sup> Mémoires de l'Académie des Sciences de Paris, 1755, p. 260.

<sup>&</sup>lt;sup>2</sup> Philosophical Transactions, vol. lii. part 1, p. 357.

<sup>&</sup>lt;sup>3</sup> In the tenth edition of the 'Systema Naturæ,' Holmiæ, 1758, which is the first in which species are characterized, we find Comatula named Asterias radiata, and thus strangely described:—"radiis duplicatis, superioribus pinnatis, inferioribus filiformibus." It was long before the difference between the true rays and the filiform cirrhi came to be understood.

memoirs of Guettard and Ellis on the recent *Pentacrinus*; nor was it corrected in the edition of the same work subsequently published (1788–1793) by Gmelin.—By Blumenbach, however, the Crinoïdea were correctly placed, in proximity with the recent *Pentacrinus* of Guettard, in his division Vermes Crustacea, with which in his later editions he associates the name Echinodermata<sup>2</sup> as a synonym; but he does not in any way recognize *Antedon* as a distinct type having a special relation to the Crinoids.

Our Antedon rosaceus was described and figured by Pennant in his 'British Zoology',' under the Linnean names Asterias bifida and Asterias decacnemos; and though no new light was thrown by him either on the peculiarities of its structure or on its affinities, yet it is deserving of notice that he specially alludes to the ventral as well as the dorsal surface being furnished with short simple rays, which are well represented in his figure. These "ventral rays," as LAMARCK afterwards pointed out, are in reality the basal pinnules of the arms, which are much longer than the rest, and (as I shall show hereafter) differ from them very remarkably in structure; but the manner in which they arch over the ventral surface of the central disk is such as to suggest to a superficial observer an analogy to the "short simple rays" or rather "cirrhi" of the dorsal surface.—The Antedon rosaceus was again described under the name of Asterias pectinata by Adams', another British zoologist of the latter part of the last century; and his notice of it, though very slight, has this remarkable merit,—that it mentions the existence of two orifices to the digestive cavity. "The body," he says, "is covered on the upper side by five unequal valves." [By this expression he seems to indicate the division of the ventral surface of the disk into five sectors by the radial furrows converging from the bases of the arms. "It is remarkable of this species that it is furnished with two apertures, one at the confluence of the valves, the other in the largest valve; their position with respect to the centre is variable; the last may readily escape observation, except when the animal chooses to elevate it above the plane of the valve." This observation seems to have been completely overlooked by those who subsequently described Antedon; its possession of distinct oral and anal orifices having been announced as a new discovery by Meckel in 1823.

The Class Echinodermata was adopted by Cuvier in his first systematic arrangement of the Animal Kingdom<sup>5</sup>; but this neither contains any recognition of the peculiarities of Antedon, nor makes any mention whatever of the Crinoïdea. Of the ignorance which still prevailed in regard to the real nature of the last-named group, we have a remarkable

<sup>&</sup>lt;sup>1</sup> Handbuch der Naturgeschichte. Göttingen, 1780.

<sup>&</sup>lt;sup>2</sup> The term Echinobermata seems first to have been introduced by Klern in his 'Naturalis Dispositio Echinobermatum' published at Dantzig in 1734; but it was limited by him to the *Echini* and their allies, now constituting the family *Echinida*. Not having been able to obtain a sight of the original edition of the 'Handbuch der Naturgeschichte' of Blumenbach, I am unable to ascertain whether the term was applied by him to include the *Asteriada* and *Holothurida* before it was so applied by Brugière in the 'Encyclopédie Méthodique' in 1792.

<sup>&</sup>lt;sup>3</sup> Edition of 1776-77, vol. iv. pp. 65, 66, tab. xxxiii. fig. 71.

<sup>4</sup> Linnean Transactions, vol. v. p. 10.

<sup>&</sup>lt;sup>5</sup> Tableau Élémentaire de l'Histoire Naturelle des Animaux. Paris, 1797.

illustration in the fact that Lamarck, in the first edition of his 'Système des Animaux sans Vertèbres' (1801), ranged them, as Linneus had done, among his "Polypes à rayons coralligènes," by the side of Gorgonia, Umbellularia, and Pennatula; apparently under the influence of the original suggestion of Ellis, and of the erroneous surmise of Guettard, who, however, nowhere goes so far as to affirm that the branching arms of his "Palmier marin" actually bear Polypes. It is not a little surprising that, with the very specimen of the recent Pentacrinus Caput-Medusæ described by Guettard under his eyes in the Museum at the Jardin des Plantes, Lamarck should have failed to recognize its close relationship to Antedon, a type which, as we shall presently see, specially attracted his attention.

The first among post-Linnean zoologists who recognized the claim of this form of Sea-star to a distinct generic rank, on account of that difference from all others in its plan of structure which had been recognized by Llhuyd and Linck, seems to have been M. Fréminville, who in 1811 thus clearly defined the genus, to which he gave the designation Antedon:—"Animal libre, à corps discoïde, calcaire en dessus, gélatineux en dessous, environné de deux rangées de rayons articulés, pierreux, percés dans leur largeur d'un trou central; ceux du rang supérieur plus courts, simples, et d'égale grosseur dans toute leur longueur; ceux du rang inférieur plus longs, allant en diminuant de la base à la pointe, et garnis dans toute leur longueur d'appendices alternes également articulés; bouche inférieure et centrale;"-referring for his illustration to the figure in the 'Encyclopédie Méthodique' (pl. cxxiv. fig. 6), which obviously represents the Stella decaenemos rosacea of Linek. Shortly afterwards (1814), and apparently in ignorance of Freminville's definition, Dr. Leach characterized this type under the generic name Alecto<sup>2</sup>. Both these designations, therefore, have a preferential claim to that of Comatula, which was not applied to the genus by LAMARCK until the publication of the second edition of his 'Animaux sans Vertèbres' in 1816. This claim was recognized in regard to Alecto by Cuvier, who gave this name the preference to Comatula; and also at one time by Professor Joh. Müller, who substituted Alecto for Comatula in many of his communications to the Berlin Academy; though he afterwards abandoned it in favour of Comatula (in ignorance, as it would seem, of the characterization of the genus by Fréminville), the name Alecto having been in the mean time assigned to a genus of Polyzoa established by Lamouroux, and having come to be generally received as its designation. Professor Müller's adoption of the name Alecto seems to have led to its employment by Scandinavian Naturalists, who have continued to use it, notwithstanding its abandonment by Professor Joh. Müller. It is clear, however, that if we are to put aside LAMARCK's name on the ground of priority, we must go back, not to Alecto, but to Antedon; and as Fréminville's definition of the genus is at least as correct as that of LAMARCK, it would be contrary to the rules of Zoological Nomenclature, as now understood and acted on, to pass it by. Notwithstanding the appropriateness of

<sup>&</sup>lt;sup>1</sup> Nouveau Bulletin des Sciences, Société Philomathique, tom. ii. p. 349.

<sup>&</sup>lt;sup>2</sup> Zoological Miscellanies, vol. ii. p. 62.

LAMARCK'S name, therefore, and the general acceptance it has met with, I feel constrained to follow the example of Dr. J. E. Gray, Mr. Norman, and Professor Wyville Thomson, in reverting to the previous designation given by Freminville.

Although Lamarck clearly differentiated Comatula as a generic type from Asterias, Ophiura, and Euryale, he was very far from apprehending its most essential peculiarities; and his description of it is strangely incorrect as regards one of its most prominent features, since he not only overlooked the true mouth, but described the anal funnel as the mouth, and placed it in the centre of the disk, which is contrary to the fact. "Au centre du disque inférieur ou ventral des Comatules, la bouche, membraneuse, tubuleuse ou en forme de sac, fait une saillie plus ou moins considérable suivant les espèces. Ce caractère singulier, qu'on ne rencontre jamais dans les Euryales ni dans les Ophiures, semble rapprocher les Comatules de certaines Médusaires." (Op. cit. tom. ii. p. 532.) This mistake is the more remarkable, as he expresses surprise at not finding the mouth (where it actually is) at the point of convergence of the furrows which pass from the rays along the ventral surface of the disk:-" Ce sillon, néanmoins, ne s'approche point de la bouche, et ne vient point s'y réunir, comme cela a lieu pour la gouttière des rayons dans les Astéries." He states, on the authority of Peron, that the Comatulæ habitually cling to Fuci or Zoophytes by their dorsal cirrhi, and spread out their rays in search of prey; and he goes on to affirm that they lay hold of this with their "grands rayons pinnés," and bring it to the mouth with their "rayons simples inférieurs." What he means by the last-named organs, I do not feel able to determine with certainty, since the "rayons simples" of his generic definition are "dorsaux" not "inférieurs;" and I am inclined to suppose that he attributes this function to the pinnules springing from the basal joints of the arms, which, as he correctly remarks, are "allongées et abaissées sous le ventre." I feel confident, from observation of the habits of the living animal, that these pinnules are no more employed in the prehension of food than are the principal arms; and I am inclined (as will hereafter appear, § 13) to regard that peculiarity of their character and disposition, which LAMARCK was the first to notice, as connected with the sensorial protection of the oral orifice.

In this edition we still find Lamarck ranking the Crinoïdea among Polypes; though he separates them, together with Pennatula, Umbellularia, &c., into a distinct group, that of Polypi natantes. He speaks without hesitation of their ramified arms as bearing polypes arranged in rows (!), and remarks that they are especially distinguished from Pennatulæ and other genera of the order of floating Polypes by the articulated structure of the stem and branches. "Les Encrines," he says (op. cit. p. 434), "se rapprochent de l'Ombellulaire par leur ombelle terminale et polypifère; mais leur tige et leur rameaux articulés, enfin la disposition des Polypes qui forment des rangées sur les rameaux de l'ombelle, les en distinguent fortement." It is singular that so eminent a Naturalist could have committed himself to a misstatement of fact so extraordinary as that just cited.

The publication of Lamarck's work was very soon followed by that of the first edition (1817) of the 'Règne Animal' of Cuvier, in which the Crinoïdea are included (after

the example of Blumenbach) in the class Echinodermata; being placed at the end of the family Asteriada, in immediate sequence to Gorgonocephala (Euryale) and Alecto (Antedon). And this position they have retained in all subsequent systems of classification; the only difference of opinion having been as to the intimacy of the relationship between the Crinoïdea and other stellate forms of Echinodermata.

The year 1821 constitutes an important epoch in this history; being that of the publication by J. S. Miller, a German naturalist residing at Bristol, of the 'Natural History of the Crinoïdea';—a work which laid the foundation of the scientific study which the group has since received on the part of various distinguished zoologists. Bringing together all the forms already known, and adding to these a large number first examined by himself, the author sought, in a careful comparison of their structural characters, a valid basis for their systematic arrangement; and the principles he developed have been followed (with some modifications in detail) by all who have since applied themselves to the same line of study, whilst the genera he created have been universally accepted as wellmarked natural groups. The most faulty part of his system was the nomenclature he conferred on the several pieces of which the cup and arms are composed; this being drawn from the osseous skeleton of Vertebrata, to which the framework of the Crinoïdea has no kind of analogy. At the conclusion of his description of the Crinoïdea, Miller enters upon the consideration of their precise relationship to the several types included by Lamarck in his family Stellerida; and after a careful comparison of their characters with those of the genera Asterias, Ophiura, and Euryale, he comes to the conclusion that with neither of these have the Crinoïdea any close affinity. He then proceeds to the like comparison with Comatula, the results of which, he says (p. 127), "were even more favourable than the first appearances had given me reason to hope, presenting, indeed, a conformity of structure almost perfect in every essential part (except the column which is wanting, or at least reduced to a single plate), and exhibiting an animal which would be defined with sufficient precision as a Pentacrinus destitute of the column." The species of Comatula investigated by Miller, though designated by him C. fimbriata, is closely allied to, if not identical with, the rosacea of Linck; the specimens of it which he examined were from Milford Haven. His description is generally accurate as far as it goes, but it includes little else than the skeleton. He makes no mention of the true oral orifice, except to state that he could not detect in his dried specimens the pentagonal mouth figured by Pennant; and it is obvious that, like LAMARCK, he was misled by the prominence of the anal funnel into supposing it to be the mouth. To Miller, then, is distinctly due the credit of having first maintained, since Llhuyd, upon the basis of an exact comparative appreciation of the characters furnished by the skeleton, that among all the recent Stellerida, the only type which bears any close correspondence to the Crinoïdea is Antedon (Comatula); and that its relationship to the Crinoids is so intimate as to require its being included with them in the same family. He did not, however, propose to remove this family from the Order Stellerida, being ignorant of those peculiarities in its digestive and reproductive apparatus which are now generally admitted to entitle the Crinoïdea to rank as a group of ordinal value.

The first approach to a knowledge of these peculiarities was made by Meckel, who pointed out that the alimentary canal is provided with two orifices: the mouth, which is nearly central, but inconspicuous; and the anus, which is prominent but eccentric. In ignorance, apparently, of what had been previously advanced by Meckel, Dr. J. E. Gray in 1826 drew attention to the existence of a double orifice to the alimentary canal, and to the importance of this character in classification. And in the same year a more complete elucidation of this part of the structure of *Comatula* was effected by Heusinger.

In 1827 the remarkable discovery was announced by Mr. J. V. Thompson<sup>4</sup> (by whom it had been made four years previously) of a true pedunculate Crinoid, to which he gave the name Pentacrinus Europæus, living in the Cove of Cork. His examination of its structure enabled him to affirm its intimate resemblance, on the one hand to Comatula, and on the other to the ordinary Crinoids; and it is interesting to observe that he had been led, by noticing its possession of a double orifice to its alimentary canal, to the recognition of the like conformation in Comatula—a discovery which was thus made independently and nearly contemporaneously by Professor Meckel, Dr. J. E. Gray, and Mr. J. V. Thompson. He does not limit himself to the description of that which he considers the perfect form of this organism; but gives an account, which though slight is very characteristic, of the principal phases of its development, commencing with that in which "the animal resembles a little club, fixed by an expanded basis, and giving exit at its apex to a few pellucid tentacula, no other part of the solid fabric being observable but an indistinct appearance of the perisome;" and he sagaciously adds, "From these observations connected with the growth of this animal, and by which it appears to present itself at various stages of its progress under considerable diversity of form, naturalists may learn to avoid the unnecessary multiplication of the genera and species of the Crinoïdea by giving undue weight and consideration to characters originating in the progressive evolution of individual species, and which are consequently of a transitory and delusive nature."

One of the most important contributions hitherto made to our knowledge of the anatomical structure of Antedon, was the memoir of Heusinger, 'Anatomische Untersuchung der Comatula mediterranea,' published in 1829<sup>5</sup>. This is, for the most part, extremely exact in its details, so far as these extend; being chiefly deficient in regard to points

<sup>&#</sup>x27; "Ueber die Oeffnungen des Speisekanals bei den Comatulen," in Meckel's 'Archiv für Physiol., 'Bd. VIII. (1823) p. 470.

<sup>&</sup>lt;sup>2</sup> "Notice on the digestive organs of the genus Comatula, and on the Crinoïdea of Miller," in 'Annals of Philosophy,' N. S., vol. xii. (1826) p. 392.

<sup>&</sup>lt;sup>3</sup> "Bemerkungen über den Verdauungskanal der Comatulen," in Meckel's 'Archiv für Physiol.' (1826), p. 317.

<sup>&</sup>lt;sup>4</sup> Memoir on the *Pentacrinus Europæus*: a recent species discovered in the Cove of Cork, July 1, 1823. With two plates. By John V. Thompson, F.L.S. Cork, 1827.

<sup>&</sup>lt;sup>5</sup> Heusinger's 'Zeitschrift für organ. Physiol.', Bd. III. p. 366.

which the use of the microscope alone can determine: and among the excellent figures by which it is illustrated, are admirable sectional views of the structure of the visceral disk, which much surpass those subsequently given by Professor Joh. Müller. I shall have frequent occasion to refer to Heusinger's memoir, when I come to describe the digestive apparatus of *Antedon*.

In 1834 M. DE BLAINVILLE published his 'Manuel d'Actinologie,' in which the relations of the Crinoïdea to the other members of the Order Stellerida are carefully examined and set forth. He divides that Order into three Families, Asteridea, Asterophydea, and Asterencrinidea; and of the latter he says (p. 248), "C'est à l'intéressante découverte faite par M. Thompson d'une très-petite espèce d'Encrine vivante, sur les côtes d'Irlande, et à son Mémoire à ce sujet, que nous devons la possibilité d'établir et de caractériser cette famille d'une manière convenable, en nous appuyant aussi sur le travail ex professo de M. Miller sur les Encrinites fossiles." Further on he says of Mr. Thompson's discovery (p. 256), that he "a détruit toute espèce de doute sur la place des Encrines vivantes ou fossiles, et a démontré clairement la justesse de la manière de voir de Rosinus, adoptée par Guettard, Ellis, Parkinson, et M. Cuvier, contre celle de LINNÉ, suivie par M. DE LAMARCK. Une Encrine n'est pour ainsi dire qu'une Comatule renversée, en supposant même que cette position ne soit pas également naturelle à celle-ci, ce que je suis fortement porté à penser, et qui, au lieu de se cramponner à l'aide des rayons accessoires, est fixée par le prolongement de la partie centro-dorsale." He divides his family Asterencrinidea into two groups, the free and the fixed; the only representative of the first being Comatula, whilst in the second he includes all Miller's genera of Crinoids, with the addition of the genus *Phytocrinus*, which he created for the reception of Mr. J. V. Thompson's *Pentacrinus Europæus*, regarding it (and with reason) as not properly referable to the genus Pentacrinus. He enters at length into the structure of Comatula, the skeleton of which he describes correctly enough, whilst in regard to its soft parts he falls into some remarkable errors. Thus he states that the furrow which runs along the axis and the lateral pinnules of each arm is provided with "cirrhes ventousaires," which serve to enable the animal to seize its prey; the fact being that these tentacula are not in any degree prehensile, and have no concern whatever in the acquisition of food. Again, whilst correctly describing the mouth, he states that the stomach has no second orifice, but terminates posteriorly in a blunt point; and that which LAMARCK regarded as the mouth, and which English authors had rightly taken for an anus, he affirms to have no connexion with the alimentary canal, but to be a prolongation from the "general cavity of the body," adding the suggestion that it may be the respiratory outlet, or may be subservient to the function of locomotion, or may be the termination of the oviducal canal. On this point he confesses himself unable to speak confidently, not having succeeded in discovering ovaries in the only individual which he dissected; but he surmises that in changing its place the animal may make use of its "vessie abdominale," contracting it upon the water with which it had been previously filled, after the manner of Cuttle-fish. He rightly stated that Comatulae

attach themselves to fixed objects by means of their "accessory rays" (or dorsal cirrhi), and that they extend their principal rays in every direction; but in asserting that this is "pour atteindre et pour attirer la proie vers l'orifice buccal," he simply hazards a supposition for which there is not any foundation in fact, the arms not being used for the purpose of grasping food or of conveying it to the mouth. It is obvious that M. DE BLAINVILLE was entirely unacquainted with the excellent description of the alimentary canal previously given by Heusinger; and that he stated as facts what were only his own conjectures.

Not many years after Mr. Thompson's publication of his Pentacrinus Europæus, he ascertained that it is nothing else than the young of the Comatula, to which he had previously noticed its close resemblance. This discovery he communicated to the Royal Society in a "Memoir on the Star-Fish of the genus Comatula, demonstrative of the Pentacrinus Europæus being the young of our Indigenous Species", which was read on the 18th of June 1835, but was not published in the Philosophical Transactions. The evidence which he adduces on this point is drawn from the resemblance between the most advanced specimens of *Pentacrinus* and the youngest *Comatulæ*, which is so close as to leave no reasonable doubt of the development of the former into the latter. Mr. Thompsox also describes in this Memoir the development of the ova in conceptacles formed by the thickening of the membranous expansion inside each of the first fifteen or twenty pairs of pinnæ. The ova, he says, "make their exit through a round hole on the fascial side of each conceptaculum, still, however, adhering together in a roundish cluster of about a hundred each;" and he adds "by what means these ova are dispersed, or how they become attached to the stems and branches of corallines, remain to be discovered." He surmised that the parent must be gifted with the power of placing them in appropriate situations; and that from "the dispersed and attached ova" the young Pentacrini at once shoot up,—a supposition which was extremely natural at the period he wrote, not the least suspicion that the first product of the embryonic development of the Echinodermata generally is an active free-swimming pro-embryo, having at that time been hazarded by any Naturalist.

In the same year (1835) some important observations on Comatula were published by M. Dujardin², who had watched the animal in a living state at Toulon. Like Mr. Thompson, he noticed the development of the ova in the swollen pinnules, and their escape through apertures which form in the integument. He also stated correctly that these animals habitually live attached to Sea-weeds, Zoophytes, &c.; only swimming occasionally for the purpose of changing their place of attachment. And he recognized the fact that the arms are not prehensile, and that the food is obtained through an agency altogether distinct from that of which other Star-fish avail themselves; but of that agency he gave an entirely erroneous account (which he subsequently withdrew), being ignorant of what microscopic examination has since revealed as to the ciliary

<sup>&</sup>lt;sup>1</sup> Edinburgh New Philosophical Journal, vol. xx. (1835-36), p. 295.

<sup>&</sup>lt;sup>2</sup> L'Institut, No. 119 (1835), p. 268.

action by which the ingestion of food is really accomplished. An examination of the residual matters ejected through the anal orifice enabled him to determine that these were spicules of Sponges, Bacillariæ, and remains of other microscopic organisms.

In the same year also there appeared the "Prodrôme d'une Monographie des Radiaires ou Echinodermes" of Professor Agassiz; which left the position of Comatula among the Crinoïdea, and of the Crinoïdea as a family of the Stellerida, very much the same as in Blainville's arrangement.

We next come to the memoir of Professor Joh. Müller, "Über den Bau des Pentacrinus Caput-Medusa," communicated to the Berlin Academy' on the 30th April, 1840, and the 13th May, 1841; which constitutes the most important contribution that has been made up to this time, not only to the anatomy of the Crinoïdea generally, but to that of Antedon in particular; the structure of that type having been carefully investigated by Professor Müller, with the view of throwing light on that of the parts of his specimen of *Pentacrinus* which were unfortunately deficient, as well as for the sake of determining the precise relations of these two genera. I shall have such constant occasion in the subsequent portions of the present communication to refer to the labours of my distinguished predecessor, that I shall here only express my high appreciation of their value, and my regret that he did not himself live to supply that completion and extension of them, for which he is understood to have collected materials during a visit he made to the coast of Norway, shortly before his death, for the purpose of studying Antedon in its living state. His investigation of the skeletons of Pentacrinus and of Antedon, and of the relations of their different parts as indicated by their muscular connexions, was conducted in a thoroughly philosophical spirit; and afforded the basis for a more satisfactory determination of the homologous parts in the fossil Crinoïdea than had been possible on the comparatively empirical method of J. S. MILLER. The nomenclature which he introduced has completely superseded that of his predecessor; and, with some modifications, it will probably remain as the standard by which all descriptions of Crinoïdea will be drawn. In subsequent communications to the Berlin Academy, which are all embodied in his Memoir "Über die Gattung Comatula und ihre Arten"<sup>2</sup>, he laid down the principles on which he considered that the systematic arrangement of the numerous species now known might best be founded; and he gave descriptions of these species, based on the characters thus indicated, and for the most part drawn from personal examination of the specimens contained in the principal European museums.

It was by Professor Edward Forbes that the title of the Crinoïdea to rank as a distinct *Order* of Echinodermata seems to have been first perceived; and in his 'History of British Star-fishes, and other Animals of the Class Echinodermata,' published in 1841, he constituted such an Order under the title of Pinnigrada, which he conferred upon it in conformity with his fundamental idea of classifying Echinodermata, like Arachnoder-

<sup>&</sup>lt;sup>1</sup> Abhandlungen der Königl. Akademie der Wissenschaften zu Berlin, 1841.

<sup>&</sup>lt;sup>2</sup> Abhandlungen der Königl. Akademie der Wissenschaften zu Berlin, 1847.

mata, according to "the modifications of their organs and modes of progression." He does not enter into any explicit justification of the claims either of the Crinoidea or of the Ophiurida to the ordinal rank here first assigned to them; but contents himself with remarking that "as an explanation of the true nature and relation of the Echinodermatous tribes, I prefer it to any arrangement at present used, and have accordingly followed it throughout this work." There can now be no doubt that Professor Forbes was completely justified in separating the Crinoidea from the Stellerida with which they had been previously associated; since they differ entirely from the Asterida and the Ophiurida in the conformation both of their digestive and of their generative apparatus; whilst their resemblance to those groups is only such as springs from the general disposition of the parts of their skeletons, the fundamental homologies of which are altogether diverse. And in accordance with his views, a rank corresponding to that of Echinida and Asteriada has been assigned to the Crinoidea by the general consent of subsequent systematists; as D'Orbigny', Van der Hoeven', Pictet', Bronn', De Koninck and Le Hon', and Dujardin'.

The account which Professor Edward Forbes gave of Comatula rosacea appears to have been written without any knowledge of the previous anatomical investigations of HEUSINGER, and was issued before those of Professor MULLER had been communicated to the Berlin Academy. It is for the most part confined to the external characters of the animal, which are in general correctly described, though not with the minuteness which could only be attained by a more elaborate microscopic investigation than Professor Forbes seems to have bestowed upon the details of its structure. He rightly apprehended the relative characters of the mouth and anus; and with respect to the latter he remarks, "This curious vent has been mistaken by many authors for the mouth, and has greatly puzzled others; and M. DE BLAINVILLE suggested that it might be connected with the functions of respiration or generation: but any one who examines the Comatula alive, or dissects a specimen well preserved, will not doubt it is a true vent." He made, however, a most extraordinary mistake in regard to the ovaries; for notwithstanding the very explicit statement of Mr. J. V. Thompson (which he quotes) as to the liberation of the ova from conceptacles formed by the swelling of the pinnæ, he affirms that only spermatozoa are formed in these conceptacles, and that the real ovaries are certain "round brown dots, placed in regular rows and at regular distances along the margins of the canals, on the body, the arms, and the pinne." What is the true nature of these spots, is a question which will be considered hereafter; it may be positively affirmed, however, that they are not the ovaries, since the production of the

<sup>&</sup>lt;sup>1</sup> Cours Elémentaire de Paléontologie et de Géologie Stratigraphiques. Paris, 1849.

<sup>&</sup>lt;sup>2</sup> Handbook of Zoology, translated by Professor Clark. London, 1856.

<sup>1</sup> Traité de Paléontologie, 200me Ed. Paris, 1857.

<sup>&#</sup>x27; Die Klassen und Ordnungen des Thier-Reichs. Zweiter Band. Leipzig und Heidelberg, 1860.

<sup>\*</sup> Recherches sur les Crinoïdes du Terrain Carbonifère de la Belgique. Bruxelles, 1854.

<sup>6</sup> Histoire Naturelle des Zoophytes Echinodermes. Paris, 1862.

ova in the swollen portions of the pinnæ has been seen not merely by Mr. J. V. Thompson, but by M. Dujardin, Professor Müller, Dr. Busch, Professor Wyville Thomson, and myself. The fact is that these animals are unisexual; and that while ova are produced in the conceptacles of some individuals, spermatozoa are developed within others, and are set free in the same mode.

The statement of Mr. J. V. Thompson as to the identity of his *Pentacrinus* with the young of *Comatula*, on which doubts had been cast by M. Dujardin¹, was satisfactorily confirmed by Professor Forbes. "When dredging in Dublin Bay," he says (Introduction, p. xii), "in August 1840, with my friends Mr. R. Ball and W. Thompson, we found numbers of the Phytocrinus or Polype-state of the Feather-star, more advanced than they had ever been seen before, so advanced that we saw the creature drop from its stemand swim about a true Comatula; nor could we find any difference between it and the perfect animal, when examining it under the microscope." He did not, however, add anything to the account previously given by Mr. J. V. Thompson of the successive stages of development of this Pentacrinoid larva; and his description of the structure of its calcareous stem is very far from being accurate, as I shall have occasion to show hereafter.

The remarkable discoveries of Professor Müller and other observers in regard to the larval or pro-embryonic forms of Echinida, Asteriada, and Ophiurida, naturally led to the suspicion that some corresponding form of free-swimming pro-embryo must be the first product of the egg of Antedon; and that this probably gives origin to the Pentacrinoid larva by a process somewhat similar to that by which the young Echinus originates from its "pluteus," or the Asterias from its "bipinnaria." To the solution of this problem Dr. Wilh. Busch<sup>2</sup>, a pupil of Professor Müller, applied himself in 1849; and he was fortunate enough to discover such a free-swimming pseudembryo, somewhat Annelidan in its form; though he did not succeed in tracing it beyond its earliest stages, or in showing how the Pentacrinoid larva originates from it. It is probably through not having done so, that his interpretation of his observations was in many points incorrect; as has been shown by the more recent and complete researches of Professor WYVILLE THOMSON3, who has worked out this part of the developmental history of Antedon with a completeness that leaves scarcely anything to desire, and who (in accordance with my request) has not only traced the metamorphosis of the free-swimming pseudembryo into the pedunculate Crinoid, but has carried on the description of the latter to the stage at which my own observations best enable me to take it up.

In 1856 an account was published by Professor Sars of the Pentacrinoid stage of Antedon Sarsii; but as the principal points of interest in this communication have already been noticed in Professor Wyville Thomson's Memoir (p. 516), I need not

<sup>&</sup>lt;sup>1</sup> L'Iustitut, No. 119 (1835).

<sup>&</sup>lt;sup>2</sup> "Ueber die Larve der Comatula," in Müller's Archiv, 1849, p. 400; and in Beobachtungen über Anatomie und Entwickelung einiger wirbellosen Seethiere. Berlin, 1851.

<sup>3 &</sup>quot;On the Embryogeny of Antedon rosaceus," in Philosophical Transactions for 1865, p. 513.

here repeat them. As he justly remarks, it would appear from Professor Sars's description that the pedunculate condition is much more prolonged in A. Sarsii than in A. rosaceus; the animal being only distinguishable by the persistence of its stem from an adult Antedon.

Early in 1863 Professor Allman communicated to the Royal Society of Edinburgh<sup>1</sup> a Memoir "On a Prebrachial stage in the development of Comatula," based on the observation of a single specimen which he had obtained on the coast of South Devon; and he was the first to publish the very interesting fact that the plates first formed in the Pentacrinoid larva are the circlet of basals and the circlet of orals superimposed on them, the former constituting the calyx, and the latter forming its pyramidal roof; the only vestige of the radials, which are afterwards to constitute the essential part of the skeleton, being a set of five minute plates intercalated between the upper angles of the basals. This disposition he compares with that of the plates in certain fossil Crinoïdea, which in his opinion permanently represent a condition that is transitory in our Pentacrinoid larva. His account of the tentacular apparatus, however, bears evidence of the insufficient opportunities for observation afforded him by the possession of a single specimen; and I feel bound to state that having myself verified Professor WYVILLE THOMSON'S descriptions,—which are based on frequently-repeated observations made upon an ample supply of specimens, and these not merely in the phase of development which fell under Professor Allman's notice, but in all the preceding and subsequent stages,—I am quite satisfied of their correctness on all those points in which they differ from the descriptions of Professor Allman.

The foregoing constitute, I believe, all the contributions hitherto made to our acquaintance with the structure and physiology of *Antedon*; and it only remains for me to notice two recent works, one on the Crinoïdea, the other on the Echinodermata generally, in which its relations to the Crinoids and to other Echinoderms are discussed with all the advantage of more advanced knowledge.

The first of these is the memoir of MM. L. DE KONINCK and H. LE HON, entitled "Recherches sur les Crinoïdes du Terrain Carbonifère de la Belgique", which is much more comprehensive than its title would indicate, since it contains an elaborate History of the progress of knowledge as to the Crinoïdea generally (to which I have already had occasion to refer, p. 675), and a philosophical investigation of their Zoological relations, and of the principles on which the classification of the group should be founded. Their inquiries have led them to a modification of the nomenclature of Professor Müller, which will, I believe, be found practically convenient, and which, therefore, I shall follow in my own description. The only addition to our knowledge of the recent *Crinoïdea* which this memoir contains, is furnished by a previously unpublished communication from M. Duchassaing to M. Michelin, accompanying a

<sup>&</sup>lt;sup>1</sup> Transactions of the Royal Society of Edinburgh, vol. xxiii. p. 241.

<sup>&</sup>lt;sup>2</sup> Mémoires de l'Académie Royale de Belgique. Bruxelles, 1854.

specimen of *Pentaerinus Caput-Medusa* transmitted by him from Guadaloupe. "La bouche de l'Encrine se trouve circonscrite par cinq lèvres. Elle ne se voit que lorsqu'on a soulevé ces cinq lèvres. On voit alors que c'est un petit trou rond d'environ deux lignes de diamètre. Les lèvres ne sont libres, et ne peuvent être soulevées que de trois lignes environ. Dans le reste, elles sont adhérentes par les cinq sillons qui partent des commissures et se prolongent jusqu'à la circonférence du disque. La mastication ne s'opère pas par la bouche, mais bien par les lèvres, qui sont armées à cet effet d'une rangée de petites épines assez fortes. Quant à la nourriture, j'ai trouvé des débris de petits crustacés." This statement is important, since the imperfection of the specimen of *Pentacrinus* described by Professor Müller prevented him from giving any account of the parts about the mouth; but the correspondence of the peripheral part of the disk with that of Comatula led him to infer that the central portions are constructed on the same plan,—the validity of which inference is confirmed by the description just cited. It further appears from the reference made by our authors to the sketches of M. Duchassaing, that the mouth of Pentacrinus Caput-Medusæ is surrounded by Oral plates, similar in form to those which exist in the Pentacrinoid larva of Antedon, though no trace of them is to be found in the adult. I do not, however, regard the evidence as yet sufficient to establish this conclusion.—In regard to the fossil Crinoïdea, MM. DE KONINCK and LE HON made an important step in advance of their predecessors in strongly drawing attention to the single, double, or multiple anal plate, as a peculiar feature in the skeleton, introducing a bilateral symmetry in what would otherwise be regularly radial. Their determination of the nature of this plate is fully borne out by its position in the Pentacrinoid larva of Antedon, although, like the oral plates, it is wanting in the adult.

Of the recent systematic treatise by MM. Dujardin and Hupé on the Echinodermata generally, it is only needful to say that whilst it furnishes a convenient résumé of previous researches upon the Order Crinoïdea and upon the genus Comatula (which, as in D'Orbigny's arrangement, is taken as the type of a distinct Family, Comatulide), it adds nothing to our knowledge of them. In their systematic arrangement and description of the species of Comatula, these authors for the most part follow Professor Müller.

### III.—EXTERNAL CHARACTERS, AND HABITS:—SYNONYMY.

1. In common with other members of the Family Comatulde, our Antedon may be described generally as composed of a central disk, from which radiate ten slender arms, fringed with pinnules along their entire length (Plate XXXI.). The disk contains the whole of the proper Digestive apparatus, which forms a lenticular mass lying in the hollow of a shallow calcareous basin or Calyx, and entirely exposed on its oral surface,

<sup>&</sup>lt;sup>1</sup> Histoire Naturelle des Zoophytes Echinodermes, comprenant la description des Crinoïdes, des Ophiurides, des Astérides, des Échinides, et des Holothurides. Par M. F. DUJARDIN et M. H. HUPÉ. (Suites à Buffon.) Paris, 1862.

which is covered only by the membranous Perisome. The centre of the visceral disk is occupied by the Mouth (Plate XXXII. fig. 3, m), which is small and slightly prolonged into five angles; and is surrounded by five somewhat elevated valvular folds, beneath the free edge of each of which is to be seen a row of minute tentacula. From the mouth there radiate five furrows channelled out in the perisome, and having elevated borders scolloped so as to form a series of minute valvules, from beneath each of which issues a cluster of three tentacles; these furrows soon bifurcate, and thus ten furrows are formed, of which one is continued on to the ventral surface of each of the arms in the extension of the perisome which clothes it. In the space between two of these furrows we see the large projecting vent or Anus (a), the shape of which differs much according as it is full or empty; sometimes its aperture is so completely closed as to be scarcely discernible, though the tube below is widely distended; whilst in other states we find the aperture patent, its edges everted and crenate, and the tube leading to it quite shrunk and flaccid.—On looking at the dorsal or aboral face of the central disk, which in the living state is ordinarily the inferior, we find it in great part concealed by an assemblage of jointed and uncinate Cirrhi, radiating from a central tubercle to which they are articulated (Plate XXXII. fig. 4), and extending even beyond the margin of the disk: the number of these ordinarily ranges in a full-grown specimen between twenty and thirtytwo; and each of them normally consists of about sixteen segments. When these have been removed, we find the under surface of the calyx to be composed, as shown in Plate XXXII. fig. 1, of a single convex Centro-dorsal plate (c), having a somewhat pentagonal margin, within which are two or more rows of sockets for the articulation of the cirrhi, whilst the central space, which bears no cirrhi, is somewhat flattened. Along the five sides of this pentagon we see five pieces  $(r^2)$  having their proximal and distal margins nearly parallel, but their surfaces convex; these are the Second Radials, the First being entirely concealed by the Centro-dorsal. And to the distal margins of the second radials are attached five pieces (r3) of nearly triangular form; their basal margins rather exceeding in length the distal margins of the second radials to which they are applied; whilst each of their inclined sides bears the first segment  $(br^i)$ of an Arm: these triangular pieces are the Third or Axillary Radials. The spaces between the diverging Radials, and between the basal segments of the Arms as far as the fourth, are filled up by the membranous Perisome, which thus completes the floor of the calvx. Sometimes, however, we find minute plates imbedded in the substance of the perisome, at the angles between the second radials (§ 9).

2. Each Arm is composed of a long series of calcareous segments, of which the dorsal surface is exposed like the dorsal surface of the calyx, whilst the ventral surface is clothed with an extension of the ventral perisome, carrying with it an extension of the radial furrows and their tentacular apparatus. With certain exceptions, hereafter to be noticed, every segment of the arms bears a jointed Pinnule, which repeats on a smaller scale the same structural features; and the furrows which pass from the disk to the arms, send branches also from the arms to the pinnules, which are continued to their

extremities. Along the borders of these furrows there extend from the inner margins of the valvular folds which fringe them, groups of delicate tubular tentacula; each group consists of three, of which one is peculiarly extensile.—The pinnules are borne on the opposite sides of the successive segments of the arms, so that they present an alternate arrangement. Those belonging to the basal segments of the arms (Plate XXXII. fig. 3) assist in supporting the visceral mass, and during life they are observed to arch over the disk (Plate XXXII. A) instead of projecting laterally like the rest; they are, moreover, peculiar in being about twice as long as those which succeed them, and in being entirely destitute of the tentacular apparatus. The succeeding pinnules, at the season of reproduction, become turgid in consequence of the development of the ovaries or testes in their substance, as already described by Professor Wyyille Thomson.

- 3. When the visceral mass has been removed from the calyx, which is very easily accomplished by tearing away the perisome that closes round its margin, we find the floor of the basin (Plate XXXII. fig. 2) nearly smooth, but depressed in the centre, where there is a passage through the calcareous pentagon formed by the union of the First Radials, which passage is occupied by a soft pedicle. This pedicle we shall hereafter find to establish a connexion between the visceral mass and certain structures contained in the cavity of the centro-dorsal plate; and it is to be regarded as the residue of the original Crinoidal axis. At a little distance from the central passage we see five pairs of Muscles arranged pentagonally; these pass between the first and the second Radials. On the distal side of each of these we see two pairs of muscles, diverging from each other; these pass between the third Radials and the first Brachials,—the second and third Radials being connected by ligamentous union only (see § 37 and Plate XXXIV. fig. 2).
- 4. The Colour of our Antedon varies greatly. Commonly it is that which its trivial name rosaceus implies; but the crimson frequently deepens to a rich damask hue, especially during the breeding-season; whilst it very frequently gives place to white on portions of the disk and arms, so that the animal has a beautifully variegated aspect. Sometimes, again, the predominant hue is a rich orange, and this may be variegated with white or crimson, or with a bright sulphur-yellow. This last is often the first colour assumed by the Pentacrinoid larvæ, when not far from the termination of their pedunculate stage.
- 5. The Size of our Antedon also varies within a wide range. Its usual diameter from tip to tip of its extended arms may be from 4 to 5 inches, but specimens exceeding this limit are by no means uncommon; and I have occasionally met with specimens as much as 9 inches in diameter. As I am certain that these last were identical in structure with the ordinary type, I cannot regard an excess of size as affording adequate ground per se for specific differentiation.

#### SYNONYMY.

6. Referring to the memoir of the Rev. A. M. Norman "On the Genera and Species of British Echinodermata" for definitions of the Order Crinoidea, the Family Ante-DONIDLE, the Genus Antedon, and the Species rosaceus, I have now to state my views on its synonymy. As to this I am not able to speak with the positiveness I could desire, since my investigations, though prosecuted over a considerable Geographical range, have not yet satisfied me as to the *limits of variation* in this type. In this, as in many similar cases, points of difference which seem extremely well marked when the most divergent examples from remote localities are compared, are found, when a sufficiently large number of examples from intermediate localities are examined, to present gradational modifications which go far to destroy their value as specific characters. And this will be found especially the case with those characters which rest on degree of development. Thus I can attach little value to the flattening of the Centro-dorsal plate (§ 22) in one type, and its uniform convexity in another,—or to the nakedness of the flattened portion in the former, whilst the whole surface is covered with dorsal cirrhi in the latter;—when I find that in the early stage of both, the centro-dorsal plate is uniformly convex and entirely covered with dorsal cirrhi, so that young specimens of the two could not be differentiated. Nor can I adopt as characters of specific difference such variations in the number of Dorsal Cirrhi, the number of their joints, the proportion of the length of these joints to their breadth, and the form of their terminal claw, as I occasionally meet with among the cirrhi of specimens from the same locality resembling each other in all other respects; the shedding and renewal of these cirrhi continuing, in my opinion, through

<sup>1</sup> The following are given by Mr. NORMAN (Annals of Natural History, 3rd Series, vol. xv. p. 102) on the authority of Professor Waville Thomson, as the diagnostic characters of Antedon rosaceus: -- "Perison of the disk naked, or with scattered tubercles containing groups of radiating calcareous spicules. Centro-dorsal plate convex, flattened at the apex, its sides covered with dorsal cirrhi; but the central flattened portion, of greater or less extent, naked. Cirrhi 14-18-jointed; the joints short, the longest but little longer than broad. Terminal claw sharp and curved; penultimate joint with a short pointed opposing tubercle, which is not developed into a claw. Proximal pairs of pinnules at least twice as long as those succeeding. Ovaries short and rounded. Usually, when mature, without any trace of interradial plates; frequently, however, with groups usually of three perisonatic interradial plates in the spaces between the radial axillaries. Colour crimson, scarlet, or mottled. Average size 4½ inches from tip to tip of arms."—Of Antedon Milleri the following are given as characters:-" Perisom of the disk with scattered warts, supported by groups of diverging spicules. Centrodorsal plate uniformly convex, and entirely covered with dorsal cirrhi. Cirrhi 15-18-jointed; the longest of the joints about once and a half as long as broad. Terminal claw curved and acute; penultimate joints without a trace of an opposing process. Proximal pinnules greatly longer than those succeeding them. Ovaries long and narrow, extending over more than half the length of the pinnules. Groups of interradial plates occupying the spaces between the radial axillaries. Of a rich brown or reddish-tawny colour. Average size 11 inches from tip to tip of the arms."—None of these characters appear to me sufficient for the differentiation of the two species to which they are respectively assigned, save the form of the ovaries, which (as Professor WYYILLE Thouson assures me) constitutes a strongly marked feature in each, and is not liable to gradational variations like Size, Colour, the form and relative abundance of the Perisomatic plates, or to variations connected with grade of development like others alluded to above.

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the whole life of the animal; and the several cirrhi of the same individual often presenting very marked differences in size and proportions ( $\S\S$  26–30). Even a character which in the first instance appeared so definite as the presence of interradial plates in one type (as in the Comatula fimbriata of J. S. Miller), and their entire absence in another (the Comatula rosacea of Fleming and Edward Forbes, the Antedon decameros of Gray, the A. rosaceus of Norman, Wyville Thomson, and myself), has proved unreliable, as I shall hereafter fully explain ( $\S$  39). And thus I am led to suspect that the range of variation in this type is very wide, and that the more extended the comparison of specimens from different localities and from different depths, the more reason there will appear for assigning only a varietal rank to several types which are at present-accounted different species.

7. As there can be no reasonable doubt that the type which forms the subject of this memoir is the one described by Linck' under the name Stella decacnemos rosacea, "propter corporis fabricam rose similem," and as the treatise of Linck is the foundation of all our scientific knowledge of the group of Sea-stars, his specific name has a preferential claim to our acceptance, which has been already recognized by Fleming 2, BLAINVILLE<sup>3</sup>, and Edward Forbes<sup>4</sup>. With Edward Forbes I am disposed to consider the Stella decacnemos barbata of Linck (the fimbriata of Barrelier, whose figure and description he cites) as specifically identical with his rosacca, although Fleming, LAMARCK, and BLAINVILLE rank it as distinct; while DUJARDIN'S (upon what grounds I cannot discover) ranks it with the Actinometra pectinata of Joh. Müller. It is impossible to say with certainty whether the Decacnemos crocea zaffarana Neapolitanorum of LINCK, the δεκαδασυακτινοειδής of Fabius Columna, is anything else than a larger form of the same, the description given of it not being sufficiently minute to enable its specific characters to be positively determined; and it may not improbably be the Antedon Milleri of Norman and Wyville Thomson. With Professor Edward Forbes, also, I consider both the Asterias bifida and the Asterias decacnemos of Pennant<sup>6</sup>, and the Asterias pectinata of Adams7 to belong to the same specific type, since their descriptions and figures do not accord with the characters of either of the other British Comatular: by Lamarck, however, the Asterias decacnemos of Pennant and the Asterias pectinata of Adams are identified with the Decacnemos barbata of Linck, which he cites as Comatula barbata. Our Antedon rosaceus is undoubtedly the Alecto Europæa of Leachs; and there cannot, I think, be any question of its identity with the Comatula Mediterranea of LAMARCK<sup>9</sup>. Under one or other of these two names this type is referred to in the principal Continental Monographs in which it is specially mentioned; the first being used by Professor Joh. Müller in his memoir "Ueber den Bau des Pentacrinus Caput-

<sup>&</sup>lt;sup>1</sup> De Stellis Marinis, p. 55, tab. xxxvii. fig. 66.

<sup>&</sup>lt;sup>3</sup> Manuel d'Actinologie, p. 248.

<sup>&</sup>lt;sup>5</sup> Histoire Naturelle des Zoophytes Echinodermes, p. 210.

<sup>7</sup> Linnean Transactions, vol. v. p. 10.

<sup>9</sup> Animaux sans Vertèbres, 2nd Ed., tom. iii. p. 210.

<sup>&</sup>lt;sup>2</sup> British Animals, p. 490.

<sup>&</sup>lt;sup>4</sup> History of British Starfishes, p. 5.

<sup>&</sup>lt;sup>6</sup> British Zoology, vol. iv. pp. 65, 66.

<sup>&</sup>lt;sup>8</sup> Zoological Miscellanies, vol. ii. 1814, p. 62.

Medusæ"; whilst the second is adopted by Meckel², Heusinger³, Sars¹, Dujardin⁵, and Professor Joh. Müller in his memoir "Ueber die Gattung Comatula und ihre Arten". Professor Wyville Thomson regards the Comatula fimbriata of J. S. Miller¸, which is described under the name C. Milleri by Prof. Joh. Müller, as probably identical with the Antedon Milleri of which I have already cited his definition (§ 6, note); Miller's figure and description of it, however, seem to me scarcely sufficient to remove the doubt suggested by its locality (§ 39) whether it is anything else than the variety of A. rosaceus which is characterized by the presence of interradial plates. I am disposed to identify our Antedon rosaceus with the Comatula adeonæ of Delle Chiaje'. But it must not be confounded either with the Comatula fimbriata or with the C. adeonæ of Lamarck, Joh. Müller, and Dujardin, or with the C. rosea of Joh. Müller and Dujardin, which are distinct types. It is probably identical with the Alecto petasus of Von Düben' and Koren.

8. The synonymy of our Antedon rosaceus, therefore, I consider to be as follows:—

Stella decacnemos rosacea, Linck.

? Stella decacnemos barbata, Linck.

Asterias bifida, PENNANT.

Asterias decacnemos, Pennant.

Asterias pectinata, Adams.

Alecto Europæa, Leach, followed by Joh. Müller.

Comatula Mediterranea. Lamarck, followed by Meckel, Heusinger, Sars, Dujardin, and Joh. Müller.

? Comatula barbata, LAMARCK, followed by Fleming.

? Comatula fimbriata, J. S. MILLER.

Comatula rosacea, Fleming, Blainville, and Edward Forbes.

Comatula decacnemos, J. V. Thompson.

? Comatula adeonæ, Delle Chiaje.

? Comatula Milleri, Joh. MÜLLER.

Alecto petasus, Von Düben and Koren.

Antedon decameros, GRAY.

The young pedunculate form of Antedon rosaceus, moreover, received from its discoverer, Mr. J. V. Thompson, the designation Pentacrinus Europaus, and from Blannville that of Phytocrinus Europaus; whilst Fleming proposed for it the designation Hibernula.

- <sup>1</sup> Abhandl, der Königl, Akad, der Wissenschaften zu Berlin, 1843, p. 177.
- <sup>2</sup> Archiv für Physiologie, 1823, p. 470.
- <sup>5</sup> Meckel's Archiv, 1826, p. 317; and Heusinger's Zeitschrift für organ, Physiol., Bd. III. p. 366.
- <sup>4</sup> Beskrivelser og Jagttagelser, &c. Bergen, 1835.
- <sup>5</sup> L'Institut, 1835, p. 268; and Hist. Nat. des Echinodermes, Paris, 1862.
- 6 Abhandl, der Königl, Akad, der Wissenschaften zu Berlin, 1847.
- <sup>7</sup> Natural History of Crinoidea, Bristol, 1821, p. 132.
- <sup>8</sup> Animali senza Vertebre del regno di Napoli.
- <sup>9</sup> "Ofversigt of Skandinaviens Echinodermer," in Königl. Vetensk. Akad. Handl. Stockholm, 1844.

# HABITS.

9. The usual habitat of Antedon rosaceus appears to be water of from ten to twenty fathoms' depth; though it is found sometimes in shallower, and sometimes in deeper water. My experience agrees with that of Professor E. Forbes, that the largest specimens are obtained from deep water. The animals are generally brought up by the dredge either actually clinging to Sea-weeds (usually Laminaria) or to Zoophytes or Polyzoa, or in such association with them as suggests the idea that their detachment has been effected in the act of dredging. For reasons I shall presently give, I cannot by any means assent to the statement of Mr. J. V. Thompson', that "this curious Star-fish is an animal not only free, but leading the most vagrant life of any of the tribe with which it has been hitherto associated by naturalists,—at one time crawling about amongst submarine plants, at others floating to and fro, adhering to thin fragments by means of its dorsal. claspers, or even swimming about after the manner of the Medusæ." It is quite true that, as stated by Mr. J. V. Thompson, and confirmed by Professor Edward Forbes, an Antedon placed freely in water will swim with considerable activity, moving back foremost by advancing five arms at a time, and then the alternate five; in fact I do not know any animal of which the movements are more graceful than those of the "feather-star" (as Professor Edward Forbes appropriately called it). But I am quite satisfied from repeated observations that these movements are not habitual to the animal, and are to be regarded only in the light of a restless search after a new attachment, being kept up no longer than is requisite for obtaining this. If an Antedon be placed in a large basin of seawater, having smooth sides and not containing any object of which its dorsal cirrhi can lay hold, the swimming action may continue (with occasional intermissions) for several hours. But if a rough angular stone, a Sea-weed, a Zoophyte, a cluster of Serpulæ, or anything to which its dorsal cirrhi can attach themselves (Plate XXXI.) be placed in the basin, the Antedon settles itself upon this, and if the attachment proves suitable, the creature seldom changes it. I have kept a number of Antedons, without any other animals, in the same Vivarium for several weeks together; and I have observed that the places of individuals which I could distinguish by some peculiarity of colour, were scarcely at all altered during the whole period,—the amount of change, in fact, being little more than would have been exhibited by an equal number of Actiniae. One fine specimen I particularly noted as having firmly attached itself by the grasp of its dorsal cirrhi to the tube of a Serpula; and this it did not let go during the whole time of its captivity.

10. Thus, as regards the ordinary fixedness of its position, the condition of the adult Antedon only differs from that of its Pentacrinoid larva in this; that whereas the latter necessarily remains fixed to the spot to which the base of its pedicle was originally attached, the former can quit its hold when its attachment is no longer suitable to its requirements, and can move from place to place in search of another. How intimate, moreover, is the functional relation between the dorsal cirrhi of the adult Antedon, and the stem of its Pentacrinoid larva, further appears from the fact that the cirrhi only

<sup>&</sup>lt;sup>1</sup> Edinb. New Philos. Journal, vol. xx. (1835-36) p. 296.

make their appearance in the latter part of the Pentacrinoid stage (as will be seen by a comparison of figs. A, B, C, D, E in Plate XXXIX. fig. 1), in preparation for that detachment of the "summit" from the stem, which thenceforth changes the condition of the animal from the fixed to the free. Notwithstanding that change, the life of the adult Antedon is habitually passed (I feel justified in asserting) so nearly in the same degree of fixedness as that of its Pentacrinoid larva, that it may almost equally be regarded as representing the life of the typical Crinoidea. If the creature ever quits its attachment, save on account of the unsuitableness of its position, it is probably during the period of sexual activity, at which it seems more frequently errant than at any other stage of its life except the earliest.

11. In regard to the ordinary condition of the Arms, there is much the same variety as is seen among Actiniæ with respect to the expansion of their tentacles. Sometimes the arms and their pinnæ are stretched out quite straight to their full length, and almost entirely in the same plane, so as to present an appearance of rigidity; whilst sometimes, still remaining fully extended, they are more or less closed together, so as to give to their whole expanse the shape of a funnel more or less deep, with the central disk at its bottom. More commonly, however, some of the arms curve either obliquely or towards the ventral surface; and this ventral curvature may be so great that the arm forms a spiral which reminds the observer of the unfolding frond of a Fern. Occasionally all the arms are seen to be thus coiled, so that the diameter of the animal is reduced to not more than one-third of that which it has when the arms are fully extended. In no instance have I ever seen the arms more than slightly curved in the dorsal direction; a peculiarity which will be readily accounted for when we examine the structure of their skeleton in detail.

12. Whatever may be the purpose of the habitual expansion of the Arms, I feel quite justified in asserting that it is not (as stated by several Authors whom I have cited in my historical summary) the prehension of food. I have continually watched the results of the contact of small animals (as Annelids, or Entomostracan and other small Crustacea) with the arms; and have never yet seen the smallest attempt on the part of the animal to seize them as prey. Moreover, the tubular tentacula with which the arms are so abundantly furnished have not in the smallest degree that adhesive power which is possessed by the "feet" of the ECHINIDA and ASTERIADA; so that they are quite incapable of assisting in the act of prehension, which must be accomplished, if at all, either by the coiling-up of a single arm, or by the folding-together of all the arms. Now I have never seen such coiling-up of an arm as could bring an object that might be included in it into the near neighbourhood of the mouth; nor have I seen the contact of small animals with a single arm produce any movement of other arms towards the spot, such as takes place in the prehensile apparatus of other animals. Moreover, any object that could be grasped either by the coiling of one arm, or by the consentaneous closure of all the arms together upon it, must be far too large to be received into the mouth, which is of small size, and is not distensible like that of the ASTERIADA.

13. A special function was assigned by LAMARCK to what he terms the "rayons simples inférieures," which, as he correctly states, are nothing else than the basal pinnules of the principal arms, "qui sont allongées et abaissées en dessous." He says that these "rayons simples" serve to bring to the mouth the prey which has been captured by the "grands rayons pinnés." This assertion I cannot but consider to be purely hypothetical. It will be shown in the Second Part of this Memoir that there are such peculiarities of structure and disposition on the part of these basal pinnules which are much longer than the rest, and habitually arch over the central disk (Plate XXXI. A)—as indicate a speciality of function; but I feel confident that the function assigned by LAMARCK cannot be the true one. For not only have I failed to perceive, after long continued observation and repeated experiments, any such movements of these pinnæ as would indicate a prehensile action, but I have found reason to suspect their function to be that of sensorially protecting the soft parts which occupy the ventral surface of the disk, and of preventing unsuitably large particles from being drawn in by the oral current. For if the *ordinary* pinnules of any arm be irritated by the contact of a rod, such irritation merely produces a languid wavy motion of the arm thus acted-on, which may extend itself to others if the irritation be repeated or prolonged. But if the rod be made to irritate the long basal pinnules, all the arms (if the animal be in full vigour) immediately close together, with an energy and consentaneousness that are seen in no other movement.

14. It was affirmed by M. Dujardin (l'Institut, No. 119, p. 268) that the arms are used for the acquisition of food in a manner altogether dissimilar to ordinary prehension; for recognizing the fact that the alimentary particles must be of small size, he supposed that any such, falling on the ambulacral (?) furrows of the arms or pinnæ, are transmitted downwards along those furrows to the mouth wherein they all terminate, by the mechanical action of the digitate papilla which fringe their borders. This doctrine he appears to have subsequently abandoned; since in his last account of this type (Hist. Nat. des Echinodermes, p. 194) he affirms that the transmission of alimentary particles along the ambulacral (?) furrows is the result of the action of cilia with which their surface is clothed. Although I have not myself succeeded in distinguishing cilia on the surface which forms the floor of these furrows, yet I have distinctly seen such a rapid passage of minute particles along their groove, as I could not account for in any other mode, and am therefore disposed to believe in their existence. Such a powerful indraught, moreover, must be produced about the region of the mouth, by the action of the large cilia which (as I shall hereafter describe) fringe various parts of the internal wall of the alimentary canal, as would materially aid in the transmission of minute particles along those portions of the ambulacral (?) furrows which immediately lead towards it; and it is, I feel satisfied, by the conjoint agency of these two moving powers that the alimentation of Antedon is ordinarily effected. In the very numerous specimens from Arran the contents of whose digestive cavity I have examined, I have never found any other than microscopic organisms; and the abundance of the horny rays of Peridinium tripos (Ehr.) has made it evident that in this locality that Infusorium was one of the principal articles of its food. But in Antedons from other localities, I have found a more miscellaneous assemblage of alimentary particles; the most common recognizable forms being the horny casings of Entomostraca or of the larvæ of higher Crustacea. It is not a little curious that in the specimens of Antedon which, through the kindness of Mr. C. Stewart, I have received from Plymouth Sound, the alimentary canal is frequently almost choked up by the body of a Suctorial Crustacean with its egg-masses. As this is far too large and powerful an animal to have been drawn into the mouth by the ciliary current as an article of food, and as its body rarely shows any indication of having been acted on by the digestive power of the Antedon, I am disposed to think that it has been introduced either as an egg or as a larva, and has undergone its development parasitically where it is found.

15. There is one point in the habits of Antedon which must be regarded as of considerable importance in the determination of the office of that vast aggregate of tubular tentacula which is borne by the pinnated arms; namely, its close dependence, for the maintenance of its life, upon pure well-aërated water. The contrast in this respect between Antedon and members of the Order Ophiurida inhabiting the very same localities and brought up from the same depths, is extremely striking. For the "sand-stars" and "brittle-stars" are among the most hardy of the Echinoderms, maintaining their activity in the Vivarium under circumstances fatal to the life of most others of its ordinary inhabitants; and I have seen them moving about for half an hour in dilute glycerine, immersion in which soon kills ordinary Starfishes. On the other hand, Antedons are among the first to die, when kept with other animals in a Vivarium; and although I was at first inclined to attribute this to the circumstance of their habitually living under a much greater pressure of water than the littoral animals with which they are associated in such artificial collections, yet I soon came to be satisfied that the real explanation was to be found in their inability to sustain any deficiency in the purity of the medium they inhabit. For by placing them by themselves, in small numbers, in an adequate supply of water, and by frequently renewing this, I have succeeded in keeping the same specimens for several weeks together; and the deficiency of vigour which they showed at the end of that time, -manifested in a general flaccidity of the arms, and in a disposition to the casting-off of portions of them, -appeared quite explicable by the insufficiency of their food-supply, made evident by the progressive shrinking of the visceral mass, the ventral surface of which came at last to be concave instead of protuberant. Moreover it happened on several occasions that if a dozen specimens of Antedon were thrown at night into a large basin of water, and were left without any means of attachment, they were all found dead in the morning, conglomerated at the bottom of the basin, clinging to each other with their dorsal cirrhi, and having their arms intertwined in such a manner as to suggest the idea that they had died of the Asphyxia produced by overcrowding, after exhausting themselves in efforts to find a suitable attachment. Whilst if, in a basin of the same size and containing the same quantity of water, there

were placed, with a like assemblage of specimens, a sufficient number of rough stones to afford them all a basis of attachment, they would be all found in the morning in a state of full expansion, with every appearance of health and vigour. Hence I feel justified in concluding that in these animals the Respiratory function can only be effectually performed in a pure well-aërated medium, and that the free exposure of the arms to that medium is no less required. I may add, further, that the intermixture of a small proportion either of fresh-water or of glycerine with the sea-water in which Antedons are immersed, is very speedily fatal to them.—It will be shown in the Second Part of this Memoir that, besides the so-called "ambulacral" canal with its tentacular extensions, each Arm and each Pinnule contains an afferent and an efferent canal, in which the nutritive fluid is exposed to the aërating influence of the surrounding medium. And that this Branchial function is shared by the Tentacular apparatus also, would appear alike from the negation already given to its supposed prehensile activity, and from its own structure and relations, as will be fully shown hereafter. Such a double provision for the function of Respiration has been shown by M. DE QUATREFAGES to be very common among the Annelida.

- 16. From the foregoing observations and the reasonings based upon them, we seem justified in regarding the following as probable conclusions:—
- 1. That Antedon, so far from being an active free-swimming animal, has the same fixed habit in its mature attached as in its earlier unattached condition; so that in regard to its general manner of life, it is not less entitled in the later than in the earlier stage of its existence, to rank as a type of the Crinoids generally.
- 2. That neither the Arms and their ordinary Pinnules, nor those elongated basal Pinnules which arch over the central disk, have any prehensile action, or any direct concern in obtaining supplies of food.
- 3. That the ordinary Pinnules are specially related to the function of *respiration*, in virtue alike of their proper Branchial canals, and of the ambulacral canals and the tubular tentacula with which they are furnished.
- 4. That the elongated basal Pinnules, in which the tubular tentacula are wanting, are rather related to the function of sensorial protection than to that of prehension.

#### IV.—STRUCTURE OF THE SKELETON.

# 1. Of the Skeleton generally, with its Ligaments and Muscles.

17. The component pieces of which the Skeleton of Antedon is made up, alike in its adult condition and in every previous phase of its existence, present a remarkable accordance with each other in elementary structure; consisting throughout of that calcareous reticulation —formed by the calcification of an animal basis that seems

<sup>&</sup>lt;sup>1</sup> This reticulation appears to have been first noticed by Professor J. Müller in 1841 (Über den Bau des Pentacrinus) as constituting the skeleton of the recent Pentacrinus of the Antilles. It was more fully described by Professor Valentin in 1842 (Anatomic du genre Echinus) as presenting itself in the shell and spines of that

nothing else than non-differentiated sarcode—which I have shown (loc. cit.) to be the essential constituent of the skeleton in every type of the Class Echinodermata. The character of this reticulation is best seen either in very thin sections of any portion of the skeleton (Plate XXXV.), or in that curiously-inflected cribriform lamina (Plate XXXIII, figs. 9-11) which I have termed the "rosette" (§ 35). This is the only part of the skeleton of the adult Antedon in which the reticulation lies all in one plane; but, as Professor Wyville Thomson has already shown, even its most solid portions, such as the First Radials, make their first appearance in the same form of cribriform lamellæ (Plate XLI, fig. 1); and whilst these lamellæ increase in superficial dimensions by the extension of the reticulation from their margins, they are augmented in thickness also by an extension of the reticulation from their inner surfaces into the animal basis in which they are imbedded.—When a portion of the skeleton, either from a fresh or from a spirit-specimen, is subjected to the action of dilute nitric or hydrochloric acid, by which the calcareous network is dissolved away, a continuous film of pellucid sarcodic substance is left, presenting no other trace of structure than in being studded at regular intervals with minute granular spots (Plate XLIII. fig. 1). The precise accordance of these spots, both in size and distance, with the meshes of the reticulation, leaves little room for doubt that whilst the pellucid sarcodic substance is the basis of the calcified network itself, the granular glomeruli occupy its interspaces. From the behaviour of this basis-substance with reagents, it seems to correspond closely with the plasma of the higher animals and with the sarcode of the lower; the pellucid substance being apparently albuminoid in its nature, whilst the granular spots are partly composed of oil-molecules.

18. The pieces of the skeleton are held together by Ligaments, which consist of minute well-defined fibres bearing a strong resemblance in aspect to those of the Yellow Elastic substance, but not (like them) capable of resisting the action of strong acetic acid. The diameter of these fibres (Plate XLIII. figs. 3,  $3\Lambda$ ) does not exceed  $\frac{1}{15000}$  of an inch; they usually run straight and parallel, but sometimes cross each other obliquely. Their attachment to the pieces of the skeleton which they connect is peculiarly firm; and this firmness is found to depend, when we examine portions of the skeleton that have been subjected to decalcification, on the passage of the fibres into the basis-substance of the skeleton itself (§ 27); much as the fibres of ligaments attached to bones are continuous with their fibroid basis, or as the fibres of tendons attached to cartilages pass into their intercellular substance. From the position and action of the ligaments connecting the pieces of the skeleton of Antedon, I think it is clear that some of them are simply interarticular, having for their function to tie these pieces together, but allowing a certain

genus. And having myself independently discovered it, I was at the same period engaged in tracing it through all the leading types of the class Echinopermata, fossil as well as recent; the results of which inquiries were made known in the Annals of Natural History, vol. xii. (1843) p. 377; and more fully in the Reports of the British Association for the year 1847.

freedom of movement between them; whilst others are decidedly *elastic*, their action being to antagonize muscles, as in many other well-known cases among Vertebrate and Invertebrate animals. Where a firm union is required, without power of movement between one segment and another,—as we shall find to be the case in regard to the pieces which form the basis of the calyx,—there is no ligamentous connexion, but simply an adhesion of expanded surfaces, closely fitted to each other, and held together by the continuity of their sarcodic basis-substance.

19. The segments of the Arms and of their lateral pinnæ, and to a certain extent those of the Rays which bear them, are made to move one upon another by a highlydeveloped Muscular apparatus. This consists of fibres (Plate XLIII. fig. 4) which resemble those of the ordinary muscles of Terebratule<sup>1</sup> in their general appearance and their want of mutual cohesion. They are cylindrical, or somewhat flattened, and show no trace whatever of transverse striation (Plate XLIII. fig. 4, 1). Their diameter is about  $\frac{1}{12000}$  of an inch; and I have not been able to resolve them into more minute elements. Interspersed among them are numerous spheroidal corpuscles ranging in diameter from about  $\frac{1}{10000}$  to  $\frac{1}{6000}$  of an inch: similar corpuscles of hemispherical or clongated form are frequently to be seen adhering to the edges of the fibres by their flattened faces (a, b); and sometimes elongated corpuscles are observable, over which the border of the fibre seems continuous (c). What is the Histological import of these corpuscles, does not seem very clear. I do not find that either they or the fibres are specially affected by the ordinary reagents. The fibres expand a little at their terminations (fig. 4, a), so as to come into closer union than elsewhere; and these expanded terminations are simply applied to the surfaces of the calcareous segments to which they are attached, not passing into their substance; so that the muscular bundles are easily torn away en masse, leaving no such roughness behind as when a ligamentous connexion is similarly treated. From the entire absence of anything like Sarcolemma or Connective tissue, the fibres are very easily isolated from each other; and there is no difficulty in tracing the same individual fibres from one point of attachment to the other through the whole length of the muscular bundle, which is sometimes as much as  $\frac{1}{4.2}$  of an inch. The entire absence of any other component in the substance of these Muscles is a point of no little interest. After careful and repeated examination of them, I feel justified in stating that they show no trace either of Blood-vessels or Nerves; yet the evidence already given (§§ 9, 13) from observation of the habits of the living Antedon, shows that in energy and rapidity of muscular action it surpasses every other known animal of its class. When we come to study the Nutritive apparatus, we shall find that although no Blood-vessels pass into the substance of the Muscular bundles, their surface forms the floor of a canal filled with nutritive fluid, for the aëration of which there is a special provision in the wide expansion of the Arms. The mode in which Nervous influence is conveyed to them is a problem of greater difficulty. It will be shown in the Second Part of this Memoir,

<sup>&</sup>lt;sup>1</sup> See Mr. Hancock's Memoir "On the Anatomy of the *Brachiopoda*," in Philosophical Transactions for 1858, p. 804.

that the cord which traverses the length of the Arms between the canal just mentioned and another canal that overlies it, and which was regarded by Professor Müller as a nerve, really belongs to the Reproductive apparatus. But it will also be shown that a regular system of branching fibres proceeding from the solid cord (described by Professor Müller as a vessel) that traverses the axial canal of each calcareous segment of the Rays and Arms (§§ 34, 45) is traceable on the extremities of the muscular bundles; and reasons will be given for regarding these fibres as probably having the function of Nerves, though not exhibiting their characteristic structure.

## 2. Of the Component Pieces of the Skeleton.

- 20. In accordance with the nomenclature now generally adopted in describing the Crinoidea. I shall distinguish the pieces of the skeleton as belonging (1) to the Stem, (2) to the Calyx, and (3) to the Arms.
- 21. Stem.—As the body of Antedon, although attached by a stalk during the Crinoidal stage of its existence, becomes free by separation from this as it approaches maturity, its skeleton might not be expected to include any representative of the Crinoidal stem. Such a representative, however, unquestionably exists in the central protuberant plate, to the convex surface of which the Dorsal Cirrhi are attached, whilst its ventral surface gives support to the First Radials. The real nature of this plate was discerned by the acute Naturalist to whom we owe our first scientific acquaintance with the Crinoid type; the following description being given of it by Mr. J. S. Miller (Crinoidea, p. 129):—
  "At the base of the subglobose body of the Comatulæ exists a pentagonal unperforated plate, slightly convex externally, and concave on the inside. It is analogous in situation to the first columnar joint of the Crinoidea; but as it is not required to transmit the passage to the alimentary canal (no prolongation of the column existing in this animal), it is without central perforation". The true homology of this central plate was also dis-

The above description must be taken in connexion with that of the "Pelvis" in the succeeding paragraph. "On the margin of the pentagonal plate rests an annular plate resembling the rim of a basin, and forming with the former a basin-like cavity, which appears to occupy the place of the pelvis of the Pentacrinite. At the upper edge this' pelvis-like plate is pentagonal, having between each of the angles a horseshoe-like impression for the insertion of the first costal joint. Externally numerous auxiliary side arms [the 'dorsal cirrhi' of LAMARCK and most succeeding authors] proceed from the pelvis-like plate, which, when they are broken off or removed, show the exterior surface of the plate marked with concave impressions (the points of their insertion), each surrounded by a hexagonal rim more or less perfect, according as their situation is near the central or the marginal circumference of the plate." It would hence appear that Miller was led by his idea of the homologies of the centro-dorsal plate to regard it as composed of two pieces, one forming the bottom of the basin, the other its sides and rim. This, however, is certainly not the case; since not only does the most careful examination of the plate in its mature form show no trace whatever of such separation, but its unity is clearly shown by the history of its development.—The latter part of the above-cited description of the "pentagonal plate" is based on the idea that the canal which passes down the centre of the Crinoidal stem lodges a continuation of the Digestive cavity. This has been shown by Professor J. MULLER to be quite untrue as regards the recent Pentacrinus Caput-Meduse; and I shall hereafter show that nothing of the kind obtains in the Pentacrinoid stage of Comatula. At a time when so little was known of the Anatomy of the Echinoderm type,

cerned by Professor J. Müller, who was led by his comparison of the component pieces of the calyx of Comatula with those of the calyx of Pentacrinus Caput-Medusæ to perceive that the "centro-dorsal" or "knopf" of the former is the representative of the highest joint of the stem of the latter; the annulus formed by the adhesion of the First Radials resting in each case upon its upper surface. The correctness of this view is placed beyond all doubt by the study of the development of this "centro-dorsal plate:" for, as I shall show in more detail hereafter (Sect. V.), this plate first presents itself in a form which nowise differentiates it from the other joints of the cylindrical stem; but begins to take on an extraordinary increase in a peripheral direction at the time when the dorsal cirrhi first sprout forth, and thenceforward remains in closer connexion with the Calyx than with the rest of the Stem, from which it separates itself so soon as the dorsal cirrhi are sufficiently developed to serve for the attachment of the animal.

22. The Centro-dorsal plate has the form of a shallow basin, with thick walls, and lip turned inwards instead of outwards (Plate XXXIII, figs. 4, 5, 6). Its outer margin, without departing much from the circular form, approaches the pentagonal sufficiently to justify the designation given to it by J. S. MILLER; and the margin of its inverted rim, forming the boundary of the opening into its cavity, is also slightly pentagonal. The diameter of this plate, in a full-grown Antedon, is about 16 inch; and its whole depth .07 inch, of which about half is the depth of its cavity, and the other half the thickness of its bottom. The thickness of the peripheral portion of its wall, however, to which alone the dorsal cirrhi are attached, is about twice that of the deepest part of the basin; as is shown in the vertical section represented in Plate XXXV. fig. 2. The central portion of the convex dorsal surface, by which the centro-dorsal plate was originally articulated to the joint of the stem next beneath, is nearly flat, and shows no peculiarity. But the entire peripheral portion is marked out into distinct sockets for the articulation of the dorsal cirrhi. These sockets are more or less circular depressions, separated by intervening ridges; and from the bottom of each depression there rises a tubercular elevation having a minute perforation in its centre. About forty sockets may usually be counted in a full-grown specimen, disposed for the most part in two rows, one alternating with the other (Plate XXXIII. fig. 5). Of these sockets, however, there are usually some to which no cirrhi are attached; these, which are generally the nearest to the centre of the disk, are distinguished by the partial filling-up of their cavity, so that the intervening ridges and the central tubercles become less conspicuous, and by the absence of perforations in the latter. The meaning of this difference will become obvious, when we follow out the development of the Centro-dorsal plate and its appendages ( $\S\S$  75, 86–88), and mark the transference of the prehensile

MILLER'S hypothesis was not so untenable as we have since come to regard it; but the unhesitating tone in which the penetration of the stem by the Alimentary Canal is spoken of throughout MILLER'S Treatise, should furnish a warning against any such assumption.

The "centro-dorsal piece" of many authors is compounded of the true centro-dorsal plate and of the pentagonal base or circlet of first radials which closely adhere to it and to each other (§§ 23, 31).

apparatus from the central to the peripheral portion of its convex surface, which is effected by the successional development of new cirrhi at the growing margin, whilst those which were originally implanted around the surface of articulation with the next joint of the stem appear to be cast off.

- 23. The upper or ventral surface of the Centro-dorsal plate (Plate XXXIII, fig. 6) which is formed principally by the thick wall of the basin, but partly also by its inturned lip, is nearly flat; being slightly elevated between the angles of its external and its internal pentagons, and somewhat depressed in the intervening spaces. The elevations correspond with the lines of junction of the First Radials that rest upon it; and the depressions with the convexities of their dorsal surfaces (fig. 2). Its adhesion to the under side of the annulus formed by the First Radials is so close, that the line of junction is not readily distinguishable in a vertical section of the "centro-dorsal piece" compounded of both (Plate XXXV. fig. 1, a, a); and it is generally more easy to break away the centro-dorsal plate piecemeal, than to detach it as a whole from the annulus of first radials,—unless the composite piece has been boiled in a solution of caustic alkali, which dissolves the organic substance whereby they are cemented together. Round the margins of the internal pentagon, we commonly find five shallow depressions (Plate XXXIII. fig. 6, a, a) which correspond with the extremities of the elongated spout-like processes of the "rosette" (§ 35); these, however, are seldom as strongly marked as in the figure, and are sometimes wanting altogether.
- 24. The internal surface of the wall that bounds the cavity of the basin is marked by minute punctations (Plate XXXIII. fig. 6), which are the internal orifices of canals that proceed from the interior cavity of the Centro-dorsal plate to the centres of the tubercles in the sockets on its convex or dorsal surface. The course of these canals, whose diameter averages  $\frac{1}{500}$  of an inch, is shown in sections of the basin taken either perpendicular or parallel to its upper flattened surface (Plate XXXV. figs. 1, 4, b, b). In such sections, when sufficiently magnified, it is also to be observed that the calcareous network which forms the basis of each socket is more solid than that of the general substance of the plate; its meshes being closer, and arranged with a regularity not observed elsewhere (fig. 4, c, c). This is conformable to what is seen in the test and spines of *Echinus*; the articular tubercles of the former and the basal cups of the latter being composed of a peculiarly close calcareous reticulation. When this centro-dorsal plate is decalcified, the animal basis is found particularly firm at these spots, each socket having a membranous disk of its own, which is traversed by very fine ligamentous fibres having a radiating arrangement; and by the convergence of these fibres is formed the interarticular liga ment which binds the first joint of the dorsal cirrhus to its articular socket.
- 25. Dorsal Cirrhi.—The dorsal surface of the calyx of Antedon is ordinarily in great degree concealed by the cluster of Dorsal Cirrhi, which radiate from the convex surface of the centro-dorsal plate (Plate XXXII. fig. 4), and which extend, when straightened

<sup>&</sup>lt;sup>1</sup> See Professor Valentin's Monograph 'Anatomic du genre *Echinus*,' pp. 20, 31, figs. 16, 17, 36, 38.—My own preparations of these structures fully bear out Professor Valentin's descriptions.

out or nearly so, considerably beyond the margin of the disk. These appendages, for which it seems to me that the designation given by LAMARCE and adopted by DUJARDIN is the most appropriate, were termed by J. S. Miller "auxiliary side arms," by Blainville "rayons auxiliaires," by Professor J. Müller "ranken," and by Professor Edward Forbes "filaments, jointed appendages, or simple arms." Any name which indicates a resemblance between these cirrhi and the Rays or Arms belonging to the calyx, is most inappropriate; since the two sets of organs have no other point of resemblance than that which consists in the articulated structure of their skeleton, whilst they differ in toto as regards both their homological relations and their functional uses. The designations respectively applied to them by J. S. Miller and by Blainville were so far correct, as indicating their homology with those appendages of the stem in *Pentacrinus* which these authors distinguished by the same terms; and it is expressly stated by the former that "these arms, the formation of their joints, and their hook-like termination, resemble in every particular those of Pentacrinus Caput-Medusæ, only that they are much shorter, and formed of a less number of joints." That the "dorsal cirrhi" of Antedon have no other function than that of mechanically fixing the animal, appears alike from the extreme simplicity of their structure (which presents not the smallest trace of the complex apparatus that is extended throughout the whole of the true brachial appendages), and from observation of the animal in its living condition, as I have already shown in the description of its habits ( $\delta \delta 9$ , 10).

26. The number of the Dorsal Cirrhi in Antedon rosaceus is by no means constant, nor is their size uniform. It is by no means uncommon to find, even on the largest specimens, one, two, three, and sometimes more of these organs in a very rudimental condition; such being usually interposed between the larger ones at the extreme circumference of the Centro-dorsal plate. In order to ascertain the range of variation in this character (to which some systematists attach considerable importance in the discrimination of species), I have carefully removed and laid upon separate tablets the entire clusters of cirrhi possessed by twelve Arran specimens, which, although differing in size, all presented every appearance of maturity; and I find the respective numbers of these organs to be as follows:—

I.	21,	of which	3	were rudimental.	1	VII.	27,	of which	3	were rudimental.
II.	22,	,,	4	27	1	VIII.	29,	22	2	77
III.	25,	,,	3	29		IX.	29,	22	0	27
IV.	25,	"	7	22		$\mathbf{X}$ .	30,	"	2	,,
V.	25,	,,	3	57		XI.	32,	,,	4	"
VI.	27,	"	3	27		XII.	32,	"	1	22

Thus it appears that Professor Edward Forbes was not far wrong in stating the number of these organs to be from twenty to thirty. I cannot, however, by any means agree

<sup>&</sup>lt;sup>1</sup> History of British Starfishes, p. 7. The number of cirrhi in *Comatula Mediterranea* is stated by Lamarck at 30, by Professor Joh. Müller at 30-40, and by Dujardin at 20-26.—I have lately had the opportunity, through the kindness of Mr. J. Gwyn Jeffreys, of examining a variety of *Antedon rosaceus* from the coast of

with him in the following statement (op. cit., p. 7): "These filaments are not all alike; there are two kinds of them. The larger have fourteen joints, and a small thick, blunt, curved claw, which is smaller than the joints, and has a horny lustre: the smaller filaments have eighteen rough joints, and an almost straight claw, which is larger than the joints preceding it." I shall presently show that the first-named form is that of the fully developed cirrhus, whilst the latter (save as to the number of joints) is that of the same organ in an earlier stage of its development; and that occasionally (though rarely) the rudimental form is retained with an increase in the number of joints beyond the average. In each of eleven out of the twelve specimens, in which I have examined the cirrhi with great care, I have found the predominant number of segments, excluding the one which bears the claw, to be 15; but in at least one-third of the cirrhi in each of these specimens (excluding those which retained their rudimental characters) the number of segments is below that standard, ranging from 14 to 10, and in a few instances to 9. In the single exceptional specimen, the predominant number of segments was 16, and one cirrhus had 17 (besides the claw); and this number I have never found exceeded, though the whole number of cirrhi whose joints I have counted exceeds 300. In two cirrhi retaining the rudimental form, I have counted 17 segments besides the claw; but I have never found this number exceeded.

27. The typical form of the Dorsal Cirrhi is represented in Plate XXXII. fig. 5, a; in which we notice (1) that the cirrhus is curved along a great part of its length in the same direction as its terminal claw, the distinction being thus marked between its convex or oral and its concave or aboral border; (2) that the basal segments are short, their diameter considerably exceeding their length, and are cylindrical, or nearly so; (3) that there is a progressive increase both in the length and in the diameter of the segments as far as the 11th joint, this increase being at first so much more rapid in length than in diameter that the 5th, 6th, 7th, and 8th segments are considerably longer than they are broad, approaching the proportion of 3:2°, with some degree of lateral compression; (4) that beyond the 11th joint the length of the segments again diminishes, their diameter remaining nearly the same; (5) that the last segment has attached to it by simple suture a strong, sharp claw, and is itself prolonged at the base of this, on its aboral margin, into a short pointed opposing process. Between the segments is

Ross-shire, one specimen of which possesses 42 dorsal cirrhi of which 7 are rudimental, and another 46 of which 8 are rudimental.

<sup>&</sup>lt;sup>1</sup> The number of joints in the circhi of Comatula Mediterranea is stated by Professor J. Müller to be 18-20, and by Dujardin to be about 20.

<sup>&</sup>lt;sup>2</sup> I am particular in the statement of these proportions, because they have been employed on insufficient of grounds (as I believe) by Professor WYVILLE THOMSON as a character of specific distinction between A. rosaceus and A. Milleri.

<sup>&</sup>lt;sup>3</sup> This process, as I shall presently show, is almost always wanting in cirrhi which have not attained their full development; and as it is not unfrequently absent in such as show no other characters of immaturity, I cannot agree with Professor Wyville Thomson (loc. cit.) in regarding the possession of this opposing process as a valid specific character of A. rosaceus.

interposed a ligamentous (not muscular) substance; this is seen in the basal joints to be as thick on the oral side as it is on the aboral; but as we advance towards the middle of the cirrhus, the thickness of the interarticular substance is seen to be much greater on the aboral side, the form of the segments being so modified as to admit of considerable flexure in that direction, whereby the prehensile power of the claw is much increased. When a cirrhus is subjected to decalcification, it is found that this interarticular substance corresponds with the general sarcodic basis of the skeleton in every particular, save in the great abundance and regular distribution of its fibrous component. The fibres can be distinctly traced passing straight and direct between the articular surfaces (Plate XLIII, fig. 5), not terminating there, however, as do the muscular fibres (§ 19), but becoming incorporated with the basis-substance of the calcified segments. And it seems clear from the history of the development of these organs, that the basis-substance of the calcified segments and the interarticular substance which connects them, are originally similar; but that whilst the former is altered by the deposit of its calcareous reticulation, the latter is changed by the augmentation of its fibrous component. The connexion of the basal segment with the socket of the centro-dorsal plate to which it is articulated, is effected by precisely the same kind of ligamentous substance (§ 24).

28. When the segments are separated by boiling in a solution of potass, and their opposed faces are examined (Plate XXXIII. fig. 8), it is seen that each is perforated by an axial canal of about one-fifth of its diameter, around which is a projecting articular surface; and that on the oral and aboral sides of this projection there are two depressions for the lodgment of the interarticular ligament. In the basal segments (a), the canal with its surrounding projection is central, and the oral and aboral depressions are of equal size, or nearly so; but in the terminal segments (b) the canal and articular surface are nearer the oral side, and the ligamental depression is both larger and deeper on the aboral. This difference is still better seen in longitudinal sections of these two portions of the cirrhus respectively (Plate XXXV. figs. 2, 3); in which also we observe that the terminal claw is attached to the last segment at a, a, by a plane surface admitting of no movement, the two being held together by continuity of their animal basis-substance. When a thin portion of such a section is examined with a sufficient magnifying power, the calcareous reticulation is seen, as in other cases (§ 24), to be much closer at the articular surfaces than it is elsewhere; and in the portion of the last segment which is prolonged into the opposing process (fig. 3), the reticulation is covered with a layer of homogeneous shell-substance like that which forms the solid pillars in the spines of the ECHINIDA. Of this substance nearly the whole solid shell of the terminal claw is composed, its interior, however, being occupied by a large cavity which is continuous with the axial canal (c, c) of the cirrhus, and the inner layer of its wall having the characteristic reticular structure.

29. The Axial Canal which thus runs from the base to the apex of each Cirrhus, is continuous at its base with the canal which passes from the concavity of the Centrodorsal plate to the summit of each articular tubercle (§ 24). It was supposed by Professor

J. Müller, who first noticed its presence, to be occupied by a nutrient vessel, proceeding from an organ contained in the basin-shaped cavity of the Centro-dorsal plate, which he designated as a heart, and from which he asserted that similar but much larger vessels pass off into the Radial plates, and thence by bifurcation into the Arms. I am perfectly satisfied, however, that these axial canals are occupied by cords of unconsolidated sarcodic substance; and that the central organ from which they proceed is developed out of the original Crinoidal Axis. How far these cords are subservient to the nutrition of the organ, or to the maintenance of its vitality, is a question that will be fully considered when the structure and function of the central organ to which they are related come under review, in the Second Part of this Memoir.

30. Having thus described the structure of the typical Cirrhus and of its component pieces, I have to speak of the cirrhi whose condition departs more or less widely from that type. In almost every specimen of Antedon we find cirrhi which do not present all the characters of maturity; and there are very commonly some whose condition is quite rudimental, corresponding to that which will be described in detail when the development of the several pieces of the skeleton is being traced out (§ 66). Such a one, represented at b (Plate XXXII. fig. 5), is seen to consist of eight minute cylindrical segments, of which the basal is the largest, and of which the terminal is rounded off without any appearance of a claw. At c is shown a more advanced stage of the same rudimental form; the segments having increased in length and diameter, but without showing any other change. At d we have a cirrlus which still presents the same rudimental form of the segments, but these have increased in number to ten, and the last segment carries a small claw; and the same condition is still presented at e, though the number of segments has increased to twelve. At f, however, we not only see an increase in the size and number of the segments, of which there are sixteen besides the terminal claw, but there is an incipient bevelling-off of the opposed faces of the segments on their aboral side, which indicates an advance in development towards the mature type; and the basal segments are equalled in diameter by those which follow. It is comparatively rare, however, to find the rudimental form still exhibited by cirrhi which have attained dimensions so considerable; the shaping-out of the segments often taking place when they are still of very small size, and the terminal claw presenting its characteristic form almost from the first. This course of development is seen in the series marked g, h, i, k, l, m;—in which it is to be observed that the basal segments are even from the first of no larger diameter than the rest; that the mature proportions between the length and breadth of the segments are shown at a very early period (h); that the bevelling-off of the opposed faces on the aboral side takes place (i) when both in number and dimensions the segments are very immature; and that in a cirrhus (1) whose length and diameter do not exceed one-eighth of the normal standard shown at a, all the characters of maturity are presented by the individual segments, even to the development of the opposing process on the penultimate segment. Hence between this and the typical mature cirrhus, the only difference consists in the number and size of the segments. At n is seen

a cirrhus which consists of the typical number of segments, and which presents the general characters of maturity except as regards the form of the claw, but has not attained above three-fifths of the full length; this may obviously have been produced either by a more advanced development of the large rudimental form represented at f, or by the process of simple increase in the small mature form shown at m.—The augmentation in the number of segments I believe to be effected by the interposition of new segments at the base, this being the part at which they are of the smallest dimensions and have most the appearance of immaturity. The augmentation in size is produced by addition to every part of the surface of the segment, this being imbedded (so to speak) in the animal basis-substance, into which the calcareous reticulation extends itself from the part previously solidified. It is to the large size of the meshes of that reticulation in the rudimental segments, that the roughness of their surface is due: as they approach maturity, the reticulation formed on the exterior of the old becomes closer, so as to give greater compactness of texture and smoothness of surface; and this is especially the case, as already mentioned, with that which forms the articular faces.

31. Pentagonal Base of the Calyx.—When the Centro-dorsal plate has been detached from the rest of the Calyx (which is readily effected by boiling for a short time in a dilute solution of caustic potass), we find the basis of the latter to consist of a pentagonal disk, formed by the close mutual adhesion of the five First Radials. The composition of this disk is obvious enough when we look at the smooth dorsal surface (Plate XXXIII. fig. 2) which was adherent to the margin and inverted lip of the centrodorsal basin; the quinary division being clearly marked out by five radiating sutures. But on its ventral aspect (fig. 3) the sutures are less distinguishable, owing to the peculiar inequality of the surface. The inner portion of the pentagonal base forms a sort of funnel, that slopes inwards to the central space; and the walls of this funnel present an alternation of radiating ridges and furrows, of each of which there are ten. Five of the furrows correspond with the divisions between the component pieces; and of the ridges which bound them, one belongs to each of the two adjacent Radials. Of the other five furrows, one passes along the middle of each of the five Radials; and both the ridges which bound it belong to the same piece. The outer portion of the ventral face of the pentagonal base consists of five surfaces inclining outwards, and marked by peculiar ridges and fossæ which will be better described when the separate pieces of this disk come under view (§ 33). Turning again to the dorsal aspect, we find the central vacuity of the pentagonal disk to be occupied by a single plate of extremely delicate conformation and peculiarly inflected shape (Plate XXXIII. figs. 2, 9); which I do not find to have been noticed by any of those who have previously described Antedon, and which, for the sake of facility of reference, I shall term the Rosette. I shall hereafter show, however, that it is really a composite structure, formed by the coalescence of outgrowths from the five Basal plates which constituted the primitive foundation of the calyx (§ 59), the original plates having been themselves almost entirely removed by absorption (§ 90). Its peripheral portion is so closely applied to the internal faces of the Radials of which this pentagonal base is composed, as to seem in absolute continuity with them (Plate XXXV. fig. 1, f); whilst its central part also is frequently connected with it by delicate processes, which sometimes sprout forth irregularly from the inner margins of the component pieces of the pentagonal disk, but sometimes form a more regular ingrowth, which considerably contracts the central space on the ventral aspect of the disk (Plate XXXIII. figs. 1, 3), and becomes continuous with an annular projection from the ventral face of the rosette.

32. The Pentagonal Base may be readily separated, after continuous boiling in the potass-solution, into its component First Radials, their mutual adhesion, and their adhesion to the centro-dorsal plate, being due to the interposition of a thin layer of sarcodic substance, continuous with that which occupies the meshwork of their own calcareous reticulation. The extreme fragility of the delicate processes whereby they are severally connected with the "rosette," occasions their detachment from it when they are separated from one another. In the adult condition of A. rosaceus, the "rosette" itself is not resolved into distinct pieces by any amount of boiling; although in its immature stage it is readily separable into five component plates ( $\S$  90).—The pieces of which the Pentagonal Base is made up will now be described in detail.

33. First Radials.—Each of these pieces has a well-marked triangular form, the apical portion of the triangle, however, being deficient (Plate XXXVI. fig. 1, c, D). We may distinguish its ventral and its dorsal faces (c, D), the former looking towards the concavity of the calvx, whilst the latter is in contact with the centro-dorsal plate; its internal face (B) bordering the central space of the pentagonal disk; its two lateral surfaces (B, i, i) by which it adheres to its fellows; and its external face (A), by which it is articulated with the Second Radial. The ventral face (c) is divided by two curved ridges (d, d), bending towards each other along the median line, and there separated by a furrow, into a central and a peripheral portion, the former sloping inwards, so as to contribute to the formation of the central funnel; whilst the latter slopes outwards, so as in fact to become part of the external face of the plate. The dorsal face (D) is slightly convex, but is free from irregularity, except that there is a deep notch (h) in the centre of its inner margin. The two lateral faces (B, i, i) are perfectly flat; and their only feature is a large aperture (q, q) which each presents towards its internal margin. The internal face (B), which is comparatively small and irregular, shows near its dorsal margin a pair of large apertures (e, e), the edges of which are raised so as to leave a distinct furrow (h) between them; this furrow, which has shown itself as a notch in the inner margin of the dorsal face (D, h) is continued onwards towards the ventral margin, but is more or less interrupted by the irregular processes which extend themselves to meet the rosette (§ 31), and which not unfrequently complete these furrows into canals (Plate XXXIII. fig. 1).—The external face is divided by a strong transverse ridge  $(A, \alpha, \alpha)$  into an upper and a lower portion; and the upper is again divided by a less elevated transverse ridge, and by median continuations of the ridges already noticed on the upper surface, into two pairs of fossæ, b, b, and c, c. Of these the upper pair

are the deeper; and they afford a surface of considerable extent for the attachment of the two great flexor muscles of the Ray, which fill up the whole space between the upper transverse ridge and the convex margins of the vertical plates, having an attachment also to the prolongations d, d of those plates, which stand forth as ridges bounding the median furrow. The shallower fossæ (b, b) give attachment to interarticular ligaments, of which the special function seems to be to hold together the plates; since I have always found, in pulling them asunder, that the greatest resistance is offered at this part of their articulation. The median furrow leads down to the large oval opening (e) of the radial canal, which partly interrupts the great transverse ridge. Below this ridge is a fossa (f) extending across the whole breadth of this surface, but especially deep in its median portion, for the lodgment of the elastic ligament which antagonizes by its extensile action the action of the flexor muscles.—The general disposition of the five pairs of flexor muscles passing between the First and the Second Radials, is shown in Plate XXXIV. fig. 2,  $m^1$ ,  $m^1$ .

34. On removing the dorsal surface of the Pentagonal Base by the careful application of an acid (Plate XXXIII. fig. 1), or by making a section parallel to its dorsal surface, and in the plane of the openings which we have noticed in the internal, external, and lateral surfaces of each First Radial (Plate XXXIV. fig. 1,  $\Lambda$ , B), we find that these all belong to one system of Canals extending radially from the central space, and also forming an annulus around it. The two apertures on the internal face of each First Radial (§ 33) lead to two canals which converge towards each other, and which very quickly meet, so as to form a single canal (a, a) which passes directly towards the external margin; whilst each of the converging canals gives off a large lateral branch (b, b), which meets a corresponding branch in the adjacent radial; and thus the five great Radial Canals are intimately connected at their origin by an arrangement that reminds the Anatomist of the "Circle of Willis" at the base of the Brain.

35. Rosette.—The peculiarly-shaped circular plate which occupies the central vacuity in the Pentagonal Base (Plate XXXIII. figs. 2, 9), and which is shown detached in figs. 10, 11, may be described as consisting of a disk perforated in the centre, with ten rays proceeding from it, five of these rays (a, a) being triangular in form and nearly flat; whilst each of the other five (b, b) that alternate with these has parallel margins inflected on its ventral aspect in such a manner as to form a groove, whilst the ray curves to its dorsal aspect in such a manner as to bring this groove to the periphery of the rosette, and then terminates abruptly as if truncated. Around the central perforation we sometimes find on the ventral surface an irregular raised collar, obviously corresponding to the central passage of the annulus of the pentagonal base; but more commonly this is replaced by a number of vertical processes irregularly disposed (fig. 11). Its diameter, in a full-grown specimen, is about 045 inch. When we look at this "rosette" in situ (Plate XXXIII. fig. 9), we find that the five triangular rays are directed to the sutures between the five Radials (a, a), their apices joining the contiguous pairs of these, just between their two adjacent apertures leading to the radial

canals; whilst each of the five spout-like rays joins the intermediate portion of one of the Radials, the inflected margins of the former being applied to the borders of the vertical furrow of the latter, in such a manner that the two grooves are united into a complete canal (b, b). Notwithstanding the apparent continuity between the calcareous reticulation of the Rosette and that of the Pentagonal Base at the extremity of each ray of the former, I am disposed to think the continuity not real, since, after boiling in a solution of potass, the rosette separates itself from the Radials without any positive fracture at these points. A real continuity, however, would seem to exist between the central prolongations of the first Radials ( $\S$  33) and the discoidal portion of the rosette, these prolongations attaching themselves to it either separately, or after coalescing with each other either to a slight extent or so completely as to form the collar just described, and the junction being so complete that its separation can only be effected by fracture.

36. This "Rosette," when viewed only with reference to its own structure and its connexions with the surrounding base of the Calyx, is one of the most beautiful objects with which I am acquainted. But the interest attaching to it will be found greatly heightened, when the extraordinary process by which it is developed from the original Basals of the Pentacrinoid larva shall have been explained ( $\S\S$  89, 90); still more, when its relations to the soft parts lodged in the Centro-dorsal cavity and its Radial Canals shall have been displayed in the Second Part of this Memoir.

37. Second Radials.—Proceeding now to the other components of the Calyx, we find the Second Radial (Plate XXXVI. fig. 2) to be a somewhat discoidal plate of elliptic figure, having two nearly parallel faces, one internal or central, articulating with the First radial, the other external or distal, articulating with the Third radial. internal face (A) is divided transversely (like the external face of the first radial) by a prominent ridge (a, a) that also passes round the large oval opening of the radial canal, and is then continued on either side of the median line to the upper margin of the plate, the two approximated ridges having a furrow between them. The large depressed spaces bounded by these ridges on either side, are again marked out by secondary ridges into two pairs of fossæ corresponding with those on the external face of the first radial ( $\delta$  33). Of these the upper pair (c, c) are the deeper, and are for the most part bounded by a pair of thin lamellæ extended upwards from the proper margin of the plate, as is obvious when we examine it from the distal side (B, d, d). These lamellæ give attachment to the distal ends of the flexor muscles; while in the shallower fosse (A, b, b) are lodged the interarticular ligaments. Beneath the great transverse ridge is a broad fossa (f) that is particularly deep just beneath the opening of the radial canal (e); this gives attachment to the elastic ligament, the tension of which antagonizes the flexor action of The external or distal face (B) is divided by a vertical ridge (a, a) that the muscles. passes round the opening of the radial canal, into a pair of lateral fosse (b, b), which give attachment to the interarticular ligaments that connect the second with the third radial, no muscular bands being here interposed.

38. Third Radials.—The Third Radial, when looked-at from above or from below

(Plate XXXVI. fig. 3, c, D), has a well-marked triangular form, presenting three articular faces; of these the central or internal looks towards the external face of the Second radial, whilst the face that looks obliquely outwards on either side serves as the base of an Arm. The internal face (fig. 3, A) corresponds very closely to that with which it is articulated, being divided, like it, by a vertical ridge, that also passes round the opening of the radial canal, into two lateral fossæ. When we look at this articular margin of the Third Radials from the dorsal side (D), we observe that its two lateral portions slope away in some degree from the median prominence; and this is also seen when we look at the articulation in section (Plate XXXIV. fig. 1) or on its ventral aspect (fig. 2). Hence, when the opposed ridges of the Second and Third Radials are in contact with each other, the third radial would seem to have some power of lateral movement upon the second. As no muscles, however, pass between the second and third Radials, which are connected by ligaments only, such movement, if it really exists, can only be attributed to the general contractility of the soft parts by which these plates are invested. From the upper margin of the internal face (A) we see projecting a pair of lamellæ (d, d) which do not form part of the surface of articulation with the second Radial, but which enter into the two oblique surfaces of articulation with the first Brachials. Each of these last faces (B) is formed upon the plan just now described as presenting itself in the opposed articular surfaces of the first and second Radials, having the transverse ridge (a, a), the fossæ for the interarticular ligaments (b, b), the fossa for the elastic ligament (f, f), and the muscular fossæ (c, c) with their thin vertical lamellæ, the lamella (d') that rises from the distal angle being common to both the oblique faces. The dorsal surface of this plate (D) presents no marked peculiarity; but on the ventral (c) a considerable inequality is occasioned by the projection of the three vertical lamelle. The radial canal, as we should expect, here divaricates, one branch passing on to either arm (Plate XXXIV. fig. 1, c).

39. No trace of *Interradial* plates shows itself in the variety of *Antedon rosaceus* with which I am most familiar,—that, namely, which occurs in the estuary of the Clyde, in Strangford Lough, and in Kirkwall Bay. But in specimens from Ilfracombe and from Plymouth Sound of what, from their likeness in all other respects, I cannot but regard as belonging to the same specific type, I find certain small plates in the angles between the Second and Third Radials, which are obviously those referred to by Mr. J. S. Miller in his *Comatula fimbriata* from Milford Haven as "intercostal plates or joints". Although Miller figures only one such plate in each angle (which may be readily understood from his having only employed a low magnifying power in examining it), yet I find that, generally speaking, it is resolvable by the Microscope into a cluster of three or four small plates (Plate XXXIII. fig. 7, B), though it is not unfrequently found to consist of an aggregation of several minute bodies (fig. 7, A) scarcely larger individually than the fragments of calcareous reticulation often occurring in the ventral perisome (Part II.). Moreover I learn from Professor Wyville Thomson that in a specimen recently dredged off Shetland by Mr. Barlee, these plates were present in three of the angles, but

<sup>&</sup>lt;sup>1</sup> Natural History of the Crinoidea, Frontispiece, fig. 2, G.

were wanting in the other two. Hence I cannot but agree with him<sup>1</sup> in regarding them as non-essential parts of the skeleton, belonging to its *perisomatic* and not to its *radial* system (§ 84).

40. Arms,—Each of the ten Arms formed by the bifurcation of the Rays, is composed of a long succession of segments, gradually diminishing in diameter from its base to its termination. The number of these segments appears to me to have no definite limit; for in every case in which the arm has presented the aspect of completeness, I have found its termination exhibiting the same indications of continued growth as are manifested by it when obviously immature ( $\delta$  67). It is remarkable that although the forms and proportions of the segments vary widely in different parts of the Arm,—their length being four or five times their diameter near its extremity (Plate XXXVIII. fig. 4), less than twice their diameter about its middle (Plate XXXVII. fig. 1), and less than half their diameter near its base (Plate XXXVII. fig. 3),—this diversity almost entirely results from the progressive increase in diameter which shows itself in the segments as we pass from the extremity towards the base; the absolute length of the segments being nearly the same throughout. The average length of each segment is rather less than ·03 inch; and thus in an arm of which the total length is 4 inches, we have about 140 segments. The general plan of their conformation is everywhere the same, each segment being fundamentally a cylindrical rod, perforated by an Axial Canal; and the departures from this form have reference chiefly to the attachment of the muscles and ligaments at the articular surfaces (Plate XXXVIII. figs. 2, 4). But the diversity in the proportions of the segments in the different parts of the Arms gives a great variety to their general aspect; and it will hence be desirable to describe separately the Basal, the Middle, and the Terminal portions of the Arms.

41. Basal Portion.—The diameter of the Arms near their base in a full-grown specimen is about '07 inch; and this is maintained with little diminution for nearly a quarter of their length. When we look at them from the dorsal side (Plate XXXVII. fig. 3), we see that the inner margin (that is, the one which looks towards the other arm of the same Ray) of their first segments is so much shorter than their outer that, whilst the two articular facets of the Third Radial incline towards each other at an angle of about 80°, that angle is widened-out between the distal articular faces of the two first Brachials that rest upon it to about 130°; and that by a similar difference in the length of the inner and outer margins of the second Brachials, their distal articular faces are brought nearly into the same plane. Generally speaking, a like inequality shows itself between the inner and the outer margins of the succeeding segments, but in an alternating manner; so that their dorsal faces have the form of a succession of triangles, the apices of which point alternately to one side and the other, their vertical angles being about 40°. But there are many departures from the regularity of this arrangement; the most frequent being that which is produced by the close union of two segments having flattened articular surfaces whose plane is directly

<sup>1 &</sup>quot;On the Embryogeny of Antedon rosaceus," Philosophical Transactions, 1865, p. 540.

transverse to the axis of the arms, forming what is called a syzygy (sg),—a peculiarity which will be presently more fully described ( $\S$  50). Excepting where syzygies occur, each segment after the first bears an articulated pinnule on its wider margin; and thus the pinnules spring alternately from each margin of the arm, the total of the two series equalling in number that of the segments, the pair forming each syzygy being counted as one. The articular facets for the basal segments of the pinnules, which are seen when the Arms are viewed on their lateral or their ventral aspects (Plate XXXVII. fig. 4, p, p), each consist of a shallow socket divided by a transverse ridge, which is perforated by a minute aperture. In this basal portion of the arms, the articular facet of the pinnule encroaches on the distal articular surface of each segment; but in the Middle and Terminal portions of the Arms, we shall find that in consequence of the change of relative dimensions of the segments, the pinnules are articulated to their lateral faces.

42. Even on the dorsal aspect of the Arms (Plate XXXVII. fig. 3), we notice that the margins of the successive segments do not come into close approximation except at the syzygies (sq, sq); and the spaces between them are occupied by an elastic ligamentous substance, which antagonizes the flexor muscles. These muscles (Plate XXXVIII. fig. 10) occupy the large spaces which are seen on the ventral aspect of the Arms, when the superficial soft parts have been cleared away (Plate XXXVII, fig. 4), to lie between the apposed faces of the segments; each segment being thinned away towards its upper or ventral margin into a vertical plate, from the middle of which projects on either side a sort of keel that forms a buttress and divides each of the deep fossæ left between the successive plates into two lateral halves. Where a syzygy occurs (sq, sq), the vertical plates of the two segments that form it come into close contact, and the keel projects only from one face of each, the two apposed segments thus taking the place of the single segment elsewhere. This peculiar contrast between the dorsal and the ventral aspects of the Arms is still better brought into view by a vertical section taken a little on one side of the axis of the arm, so as not to pass through the projecting keels that divide the muscular fossæ, and only partially to lay open the axial canal (Plate XXXVIII. fig. 11). This shows that the successive segments really come into contact with each other only by the great transverse ridges which cross their articular surfaces (Plate XXXVI. figs. 4-8, a, a), and embrace the opening of the axial canal; and that the space between these ridges and the dorsal surface, which is occupied by the elastic ligament, is much larger than it appears externally to be. Of the large space between the axial canal and the ventral margin, the part nearest the canal is occupied by the interarticular ligaments which are lodged in the shallow fossæ' that are seen on each articular surface just above the transverse ridge; whilst the much longer spaces intervening between the vertical plates are entirely filled by muscular substance (m, m), the fibres passing directly from each plate to the next in front and behind, except in the case of a syzygy.

<sup>&</sup>lt;sup>1</sup> These are termed "articular facets" by Professor Müller; but I feel satisfied that they cannot come into contact with those of the succeeding segment, and that they have the character above assigned to them.

Between the canal and the *dorsal* margin are shown the large elastic ligaments. l, l. —In Plate XLIII. fig. 6 is shown a similar section of a *decalcified* Arm, passing vertically along the median plane through the axial cord (a, a); so as to bring into view the muscles (m, m) lodged in the spaces intervening between the vertical lamellae  $(s^i, s^i)$  of the successive segments, the interarticular ligaments  $(l^i, l^i)$  above the axial canal, and the great elastic ligaments  $(l^2, l^2)$  below it, lodged in the deep fosse of the bodies of the segments (s, s).—In fig. 7 is shown a longitudinal section of a *decalcified* Arm passing horizontally through the axial cord (a, a); which exhibits the oblique disposition of the elastic ligaments  $(l^2, l^2)$ , occasioned by the alternating obliquity of the segments; and also shows the interposition of the sarcodic radiations at the syzygies (sq, sq).

- 43. When the articular surfaces of the Brachial segments are brought into view by separating these segments from each other, we find them for the most part characterized by the same features as those which are presented by the opposed surfaces of the First and Second Radials ( $\S\S$  33, 37). With certain exceptions to be presently noticed, each is divided by a transverse ridge (which usually crosses it more or less obliquely) embracing the opening of the axial canal; and whilst the single deep fossa below this ridge gives lodgment to the *elastic* ligament by which the arm is extended, the pair of shallower fossæ above it serve for the attachment of the *interarticular* ligaments; whilst above these, again, are the pair of deep fossæ, formed by the recession of the vertically projecting lamellæ, in which the flexor muscles are lodged. From the peculiar shape of the brachial segments ( $\S$  41), the articular surfaces generally incline to one side or the other, instead of looking directly forwards or backwards along the axis of the arm.
- 44. It obviously results from the general conformation of the segments, the peculiar disposition of their articular surfaces, and the arrangement of the muscles and ligaments, that provision is made for very free flexion of the Arm towards the ventral aspect by the contraction of its muscles; and this flexion can take place to such an extent that the arm may in a moment coil itself into a spiral resembling that of a watch-spring. When the muscular tension is relaxed, the elasticity of the ligament on the dorsal side of each segment straightens the arm, and may even flex it in some degree in the opposite direction; such dorsal flexion, however, never takes place to any considerable extent. The arms also possess a slight power of lateral flexion, in virtue, as it would seem, of an inequality of action in the two flexor muscles of each articulation; but this flexion is very limited in amount.
- 45. The Axial canal by which each segment is perforated, carries on through the whole length of the Arms the axial canal which divaricates in the Third Radial (§ 38); and it also gives off branches which in like manner enter the bases of the Pinnules, and proceed through their successive segments to their extremities. This canal is occupied by a solid cord of sarcodic substance, which I shall hereafter show to be really, like the similar cords that fill the canals of the dorsal cirrhi (§ 29), a branch of the original Crinoidal axis.
- 46. The peculiarities presented by individual segments of the Arms are most conspi-MDCCCLXVI. 5 F

cuous in the first five, every one of which may be readily distinguished from any other and it will be desirable, therefore, to describe each of these separately.

- 47. First Brachial.—It has been already shown (§ 41) that the inequality between the lengths of the inner and the outer margins of this segment (Plate XXXVI. fig. 4, c, D) is so considerable as to compensate in great degree for the extreme obliquity of the distal face of the Third Radial, to which it is articulated; and is such as even to occasion a curtailment of the inner half of each articular surface (fig. 4, A, c). The proximal articular surface (A) presents on its outer side no special peculiarity; but on its inner side we notice at the inner extremity of the fossa for the interarticular ligament a peculiar rounded pit (g), which might be supposed to be the socket for the articulation of a pinnule. This, however, is not the case; for no pinnule is borne by this segment, and the articular sockets of the pinnules are always found on the longer sides of the Brachial segments. The muscular fossæ are carried so far back by the recession of the vertical lamellæ which bound them, as to form the greater part of the ventral face of the segment (fig. c, c, c). The distal face (B) is formed on the plan of that of the Second Radial (§ 37); being simply divided by a vertical ridge (a, a) into two lateral fossæ (b, b), in which are lodged interarticular ligaments, but no muscles.
- 48. Second Brachial.—This segment presents a certain degree of resemblance to the preceding in general form, and, like it, has its outer margin so much longer than its inner as to produce a considerable obliquity between its articular surfaces (Plate XXXVI. fig. 5, c, d). But it is here the proximal face (A) articulating with the First Brachial, which is divided (like that of the Third Radial, § 38) by a vertical ridge into two lateral fossæ; whilst the distal (B), which articulates with the Third Brachial, bears a general resemblance to the proximal face of the First, but is at once distinguished by the excavation of its outer and upper portion (trenching on the outer muscular fossa) into the articular surface for the first pinnule (p, figs. B, E). But for this difference, the Second Brachial might be easily mistaken for the First Brachial of the other arm of the same ray.
- 49. Third Brachial.—The general form of this segment (Plate XXXVI. fig. 6) is more discoidal than that of either of the preceding; but it still has a decided obliquity (figs. c, d) between its proximal and its distal articular surfaces, which is, however, in the contrary direction to that of the First and Second Brachials (Plate XXXVII. fig. 3). The proximal face (A) presents the usual arrangement of fossæ for the lodgment of muscles and ligaments; the surfaces for the attachment of muscles being here chiefly provided by the two rounded lamellæ which project from the upper or ventral margin of the segment (d, d, figs. A, B). The distal face (B) shows a peculiarity of conformation which we have not yet encountered; for it is unmarked by any prominent ridges or fossæ, being in fact almost flat, except that it presents a series of slightly elevated ridges with alternating furrows, which radiate from the opening of the central canal towards the dorsal margin. The union of this face with the opposite face of the Fourth Brachial (sg, figs. c, d, e) constitutes what was designated by Professor J. Müller a syzygy.

50. Fourth Brachial.—This segment (Plate XXXVI. fig. 7) has the same general form with the preceding, and the obliquity of its two faces (c, D) is in the same direction, the longer being again the internal. While the distal face of this segment (B) conforms to the ordinary type, and is distinguished from the proximal face of the Fourth segment (with which it might otherwise be confounded) by possessing an articular socket for the pinnule (p, figs. B, C, E), its proximal face (1) shows the same ridge and furrow arrangement as the distal face of the Third .- When we examine the Third and Fourth segments in their natural apposition (fig. 6, c, D, E), we see that the two sets of ridges are applied to each other (sq), leaving between them flattened passages that are formed by the correspondence of the furrows. The adhesion between these apposed surfaces is so close, that it can only be dissolved (like that of the First Radials to each other and to the Centro-dorsal plate, §§ 31, 32) by boiling in a solution of caustic alkali. No ligamentous substance is interposed between them; but an examination of decalcified specimens shows that the canals are occupied by radial extensions of the ordinary sarcodic basis-substance (Plate XLIII. fig. 2). The peculiar arrangement of these suggests that, like the "medullary rays" of an Exogenous Stem, they may serve to establish a communication between the "medullary axis" of this basis-substance which occupies the central canal, and the "cortical envelope" by which the surface of the segment is invested. When we come to study the development of the Brachial segments (§ 67), we shall find that the syzugies do not originate (as has been supposed by some) in an imperfect subdivision of segments, -no subdivision, perfect or imperfect, ever taking place; but that they are formed by a partial coalescence of segments originally quite distinct. For in the early stage of the existence of this animal as a detached Antedon, there is still so little specialization in the rod-like segments of the arms, that they are all nearly similar in form, have no proper articular surfaces, and are held together by nothing else than an imperfectly fibrous sarcodic substance. And whilst the majority of these gradually come to possess true articulations, and to be separated by the intervention of muscles and ligaments, a certain small proportion become more intimately united on a simpler plan, which admits of no motion between them. These syzygies are repeated at more or less frequent intervals along the greater part of the length of the arms; and as they are normally pretty constant in position in the several Arms of each individual, and in the several individuals of one species, whilst usually diverse in those of different species, it has been proposed by Professor J. MÜLLER to use them as characters of specific definition. To this it has been objected by Dujardin' that the syzygies are really variable in their number and in their mode of distribution on the several arms, especially when there has been a reparation after injury, so that on the same individual there may intervene from four to nine ordinary articulations between the corresponding syzygies. Whilst fully admitting the existence of irregularities thus originating, which are for the most part easily recognized, I am disposed to believe with Müller that there is a normal type which is constant—as regards the basal portions of the arms at least—for each species,

<sup>1</sup> Histoire Naturelle des Zoophytes Echinodermes, p. 193.

and which may thus afford valid specific characters. In Antedon rosaceus, and what I believe to be its varietal forms ( $\S\S$  6, 7), the second syzygy (Plate XXXVII. fig. 3) occurs at the junction of the 9th and 10th segments, and the third at the junction of the 14th and 15th.

51. Fifth Brachial.—We now come to that which may be regarded as the ordinary form of the segments constituting the basal portion of the Arm, and which is repeated with great uniformity except where a syzygy intervenes,—the peculiar mode of articulation existing between the First and the Second segments not presenting itself elsewhere. Each articular face (Plate XXXVI. fig. 8, A, B) presents the same disposition of transverse ridges and ligamentous and muscular fosse (a, a, b, b, c, c); and the same vertical lamellæ for the attachment of the muscles (d, d, figs. A, B, c) are common to both. The articular base of the pinnule is situated at the upper and outer margin of the distal articular surface (fig. B, p); and in this and the succeeding segments (in which its position is alternately on the inner and on the outer side) its presence always enables us at once to distinguish the distal from the proximal face of the segment. These faces are also distinguishable by the much greater inclination presented by the proximal face, the distal face being nearly vertical; this character, which repeats itself along the entire series of segments, is best seen on looking at the arm from above (Plate XXXVIII. fig. 4) or in section (Plate XXXVIII. fig. 11).

52. Middle Portion.—As we pass from the basal portion of the Arms in the direction of their termination, we find in the first instance no other change in the conformation of the segments than is brought about by a considerable diminution of their diameter without a corresponding diminution in their length (Plate XXXVII. fig. 1). in the segment of which the proximal and distal faces and the longer side bearing the pinnule are represented in Plate XXXVIII. fig. 5, A, B, C<sup>1</sup>, we recognize the same arrangement of the great transverse ridge, the deep fossa for the elastic ligament between this ridge and the dorsal margin, the pair of shallower fossæ for the interarticular ligaments on the ventral side of the ridge, and the larger and deeper muscular fossæ chiefly formed by the vertical plates rising up on the ventral margin, with the articular socket for the pinnule encroaching on the muscular fossa of the longer side, that have been described in the last paragraph. But whilst the transverse and vertical diameters of this segment are scarcely more than half those of the Fifth Brachial, the length of the longer side is rather greater than less, so as quite to equal the transverse diameter. With this change of proportions there is an increased obliquity of the articular surfaces, alike in the transverse and in the vertical direction; and thus the spaces between the lamellæ for the attachment of the muscles that pass from segment to segment remain undiminished in length (Plate XXXVII. fig. 2), although those lamellæ are brought, by the reduction in the diameters of the segments, so much nearer to the axial canal of the arm. The articular sockets of the pinnules are now quite removed from the articular surfaces of the segments; and when two segments are united by syzygy (fig. 1, sg, sg), their conjoint

<sup>&</sup>lt;sup>1</sup> These figures have been inverted by the Artist, so that the dorsal margin is uppermost.

length is but little greater than that of an ordinary single segment.—The same general proportions are maintained through a considerable part of the length of the Arm, the tendency being, however, to a further reduction in the diameter of the segments, without a corresponding reduction of their length; so that notwithstanding the increased obliquity of the articular surfaces, the muscular fosse of the proximal and distal faces of each segment, instead of being separated merely by the thin vertical lamellæ which form the floors of both, lie as it were along its ventral surface, and yet do not come into close approximation.

53. Terminal Portion.—Passing onwards to the termination of the Arms, we find a progressive diminution in the diameter of the segments, without a corresponding reduction in their length; so that their proportions now differ widely from those of the basal segments (Plate XXXVIII, fig. 4). We still observe, however, an alternating obliquity in the disposition of their articular surfaces as seen from the dorsal side; a sort of notch being left, first on one side and then on the other, which is occupied by the elastic ligament. On separating the articular surfaces, we no longer find them presenting the characteristic ligamental and muscular fossæ; but there are nearly plane surfaces above and beneath the central aperture, to which the ligaments are attached, whilst the muscles lie in elongated fossæ excavated in the ventral face of the segments (c, c, fig. 2, A, B). The articular sockets for the pinnæ (p, p) show themselves on the lateral surfaces of the segments at about the middle of their length, and are quite removed from the muscular fossæ. -Of the normal mode of termination of the Arms, I am unable-after an examination of some hundreds of specimens-to speak with certainty; for I have never met with a specimen of this animal possessing in other respects the characters of maturity, which presented such a gradational diminution in the dimensions of the terminal segments as might be fairly expected from the general plan of its structure. In a large proportion of cases the Arms end so abruptly as evidently to show that their terminal segments have been broken off. And when they do present such a termination as is shown in Plate XXXVIII. fig. 4, this has all the characters of immaturity (§ 67); and must be regarded as marking, not the completion of the growth of the Arm, but either the continuance of its normal extension, or the reproduction of the portion which has been lost.

54. Pinnæ.—The pinnules with which the Arms are fringed (Plates XXXVII. figs. 1, 2, 3, XXXVIII. figs. 4, 10, 11) are composed of articulated segments nearly cylindrical in form, and gradually tapering from their base to their extremity, which bears a peculiar segment furnished with five or six minute hooks (Plate XXXVIII. fig. 3). The size and length of the pinnules vary considerably in different parts of the Arm, those near the base being not only longer, but also stouter in proportion to their length. The first pair of pinnules, which are attached to the Second Brachial segments, are much longer than those which succeed, often in fact attaining double their length; and these, as already mentioned, are nearly always seen in the living state bending over the ventral disk (Plate XXXI. fig. Λ). The first segment, which is articulated to the Brachial

segment that bears it by ligaments only, is much shorter than that which follows it (Plate XXXVII. fig. 3); and the length of the succeeding segments presents a considerable uniformity, until we approach the termination of the pinnule, where we often find a set of segments much shorter than the rest (Plate XXXVIII. fig. 3), suggesting the idea that these are the last formed. The number of segments in the pinnules is found by no means constant, when we compare either different pinnules of the same Arm, or corresponding pinnules in different individuals. Thus the first, which from their peculiar relation to the mouth I distinguish as the oral pinnules, very commonly have about thirty-five segments; but I have not unfrequently counted as many as forty, and in one instance forty-five. And while the ordinary pinnules of the basal part of the Arm have usually about twenty segments, the number not unfrequently rises to twenty-five. In the middle part of the Arm (Plate XXXVII. fig. 1) the number of segments in the pinnules may average eighteen; and in its terminal portion we find this rapidly diminishing from sixteen to half that number (Plate XXXVIII. fig. 4). The general conformation of the individual segments closely corresponds with that of the segments of the dorsal cirrhi (§ 28). They are nearly cylindrical, but somewhat compressed on their ventral aspect; and each of them (at least in the pinnules of the basal and middle parts of the Arms of well-developed specimens) has the dorsal margin of its distal end fringed by a set of short oblique spines (Plate XXXVII. fig. 3). The articular faces of the segments are formed on nearly the same plan with those of the segments of the dorsal cirrhi (§ 28), the opening of the central canal by which every segment is traversed, being surrounded by a slightly elevated ring, sometimes extended into a transverse ridge, and a depression being left by the bevelling-away of the surface in both directions, that serves for the lodgment of interarticular ligaments. But besides these depressions, there is in each of the basal segments, at least of well-developed pinnules, a small but deep notch in the ventral margin of each articular surface, but deeper in the distal; and this lodges a minute muscle (Plate XXXVIII. fig. 10), by the action of which the pinnules can be so flexed that those of the two sides of the Arm are brought towards each other, and also towards the line of its axis,—the converse movement of extension being effected (as in the Arms) by the elastic ligaments, when the muscles are relaxed.

#### REPARATIONS.

55. It is well known to Naturalists that a remarkable degree of reparative power is exhibited by Echinodermata generally; and our Antedon, so far from constituting an exception, affords abundant exemplifications of its operation. For when we have the opportunity of examining a large number of specimens brought up together by the dredge, we are sure to meet with several which have obviously sustained losses either of entire Arms or of portions of Arms, and in which the lost parts are being reproduced on a smaller scale. We so often find that the fracture has taken place at a syzygy (Plate XXXVIII. fig. 6) that the question suggests itself whether there is any special reparative power at

this joint,—analogous to that which in the Decapod Crustacea is well known to exist in the basal extremity of the first phalanx. I am inclined to the belief, however, that the comparative frequency of fracture at the syzygies depends rather on the greater brittleness of the Arm at these points; the syzygal segments being held together only by sarcodic substance, instead of (as elsewhere) by ligaments and muscles. Certain it is that the reproductive power, instead of being limited (as in the Crab and Lobster) to one particular articulation, may be exerted at any point in the Arm, or even in the Ray. Thus we see in fig. 9 that a Ray has been torn off at the junction of the First and Second Radials; since not only the pair of Arms, but the Second and Third Radials which bear them are so much smaller than the rest, as to be obviously products of the reparative process. It is worthy of remark that the syzygies of these reproduced arms occur at the regular intervals. Another case of the same kind, in which the new Ray and Arms have attained a more advanced development, is shown in Plate XXXVIII. fig. 8, A. In other specimens in my possession, the reparation has commenced from the bifurcation of the Arms, from the articulation between the first and second Brachials, and from the articulation between the second and third; and here, again, it is interesting to remark that the first syzygy always occurs between the third and fourth segments, although there is often some irregularity (on the side of excess) in the interval between the first and the succeeding syzygies.—It is much more common, however, for only the terminal portion of an Arm to have been lost; and the new growth by which it is being replaced often affords a peculiarly good illustration of the mode in which the development of fresh segments is accomplished (§ 67).

56. It is curious that in some cases the act of reparation should be attended with Monstrosity; and this may be on the side either of excess or of defect. Of the former we have an example in Plate XXXVIII. fig. 8, B; where we see that a fracture having taken place at the articulation between the first and second Brachial segments, the new Second Brachial, instead of conforming to the ordinary type, resembles the Third or Axillary Radial, and gives support to two Arms, which have already attained a considerable development. A case of the latter is shown in the specimen represented in Plate XXXVIII. fig. 7, where the normal bifurcation of the Ray has not taken place, the Third or Axillary Radial being deficient, whilst the Second (which has about twice its normal length) bears a single Arm of full size, with its syzygies regularly repeated. Whether this monstrosity had its origin in fracture, however, may be doubted; and the like doubt may be entertained in regard to another case of "monstrosity by excess," which has presented itself to me in an oral Pinnule; a bifurcation like that of the Ray into a pair of Arms presenting itself at the second segment, so that two full-sized pinnules take the place of the ordinary single pinnule.

#### V.—DEVELOPMENT OF THE SKELETON.

### 1. General History of the Pentacrinoid Larva.

57. The study of the development of the pieces of which the Skeleton of Antedon is made up, will be best pursued in the first instance by following the general history of the development of its Pentacrinoid Larva, from the epoch at which Professor Wyville Thomson's account of it ceases, to the termination of its attached condition; since it will be in this mode that I can best make apparent the relation of the remarkable changes which the skeleton undergoes during this period, to the progressive evolution of the other parts of the fabric.

58. The nature of the objects to which the Pentacrinoid Larvæ attach themselves, varies with the locality. In Lamlash Bay, Arran, where my own studies of Antedon have been for the most part carried on, I have never found them affixed to anything else than the fronds of Laminariae (to which the adult Antedon habitually clings), or to Polyzoa or Spirorbes attached to these. But at Ilfracombe, where Laminaria are much less abundant, but where the Polyzoon Salicornaria grows in great luxuriance in the habitat of Antedon, the Pentacrinoid larvæ are found adherent to its stony Polyzoary. Mr. J. V. THOMPSON found them in the Bay of Cork "attached to the various species of Sertularia and Flustracea which occur in the deeper parts of the harbour of Cove, viz. in from eight to ten fathoms." Mr. WILLIAM THOMPSON (of Belfast) found them attached to Delesseria sanguinea. Hence I think it can scarcely be doubted that the Pentacrinoids will attach themselves indifferently to any Fuci, Polyparies, or Polyzoaries, which may abound in the habitats of the parent Antedon. Though generally scattered over the surfaces of these, so as not to be in any near proximity to each other, yet sometimes we meet with a group of several Pentacrinoids very close together, so as to present in one view all the stages in development represented in Plate XXXIX. I have one specimen in my possession, indeed, in which more than seventy Pentacrinoids, all nearly in the same stage of development, are attached to the surface of a patch of Membranipora that was encrusting a frond of Laminaria; and in another, which I owe to the kindness of Professor WYVILLE THOMSON, thirty-five Pentacrinoids, in that earlier stage which was first described by Professor Allman, are so closely clustered together that the discoidal bases of their stems have come into mutual contact, and have acquired a polygonal form. These, he informs me, were bred in his Vivarium; and the circumstances of their aggregation were not a little curious. A pseudembryo, when losing its power of locomotion, was frequently seen floating in such a manner that its incipient discoidal base spread itself out (often in a stellate form) on the surface of the water, whilst the stem and body of the rudimental Pentacrinoid hung downwards from this; and it sometimes happened that by the approximation of a number of individuals in the same condition, the stellate extensions of the disks became mutually adherent. Similar clusters were found by Professor Wyville Thomson attached to the inner surface of a dead valve of Modiola modiolus.

59. Referring to the admirable Memoir of Professor Wrylle Thomson for full details of the early development of the Pentacrinoid Larva from the free pseudembryo, I shall briefly recall the principal features which it presents when it has fully assumed the Crinoidal type.—The animal consists in the first instance of stem and calyx alone, not even rudiments of arms being distinguishable. The stem is composed of from 8 to 10 cylindrical segments, the lowest of which is articulated to a discoidal plate which forms its base of attachment; whilst the highest expands to serve as the foundation whereon the plates of the calyx are built up. The calyx completely encloses the visceral mass, its oral valves, when drawn together, meeting over the mouth; whilst, when these open out, it has the form of an inverted bell<sup>2</sup>. Its lower or aboral portion is composed of five basal plates, which form by their approximation a five-sided pyramid with its truncated apex pointing downwards; whilst its oral part is composed of five oral plates, the approximation of which forms a similar pyramid with its truncated apex pointing upwards, though they are usually erected as separate valves, to allow the oral apparatus to be projected from within them. These two pyramids are the parts of the skeleton of the calyx which first make their appearance; and the one is so superposed on the other that the plates of the oral are opposite to those of the basal pyramid. At a somewhat later period the first radials make their appearance in the spaces left by the contiguous angles of the basal and oral plates, so as to alternate with these in position. Between two of the radials, and on the same level with them, an unsymmetrical plate early shows itself, the subsequent relation of which to the vent proves it to be an anal plate. From the summits of the first radials, the second radials are next seen to bud forth between the bases of the orals; and as the circle formed by these last does not increase in diameter, whilst the ring of first radials on which it rests has become larger, the orals are relatively carried inwards, whilst the second radials project somewhat outwards.—In the latest stage described by Professor WYVILLE THOMSON, the third or axillary radials have begun to show themselves at the distal extremities of the second; and rudiments of a pair of first brachials are distinguishable at the distal extremities of the third radials3.

60. The several portions of the skeleton are imbedded in a nearly homogeneous sarcodic substance, which externally forms a perisomatic investment, and internally constitutes a lining to the calyx. The Digestive Cavity seems in the first instance to be simply
excavated in the body-substance; but as the radial plates are developed, giving an
expansion to the equatorial portion of the cup, the wall of the Stomach becomes separated from the lining of the calyx by a distinct perivisceral cavity filled with fluid, in
which the stomach seems to hang attached to the body-wall here and there by sarcodic
bands and threads. Simultaneously with the appearance of the anal plate, a slender digitate process rises from one side of the stomach and curves towards that plate; this constitutes the rudiment of the Intestine, but it has not as yet any outlet, and I believe it
to be in this stage destitute even of an internal canal, being an extension of the wall of

<sup>&</sup>lt;sup>1</sup> Philosophical Transactions, 1865, p. 513. <sup>2</sup> Ibid. Plate XXVI., figs. 1, 2. <sup>2</sup> Ibid. Plate XXVII. fig. 1. MDCCCLXVI. 5 G

the stomach but not of its cavity.—The mouth of the bell, when the oral valves are expanded, is entirely occupied by the oral apparatus. The mouth itself is a wide orifice, allowing the interior of the stomach to be plainly seen when looked into from above; and this is surrounded by a prominent ring from which arise the oral tentacles'. This ring is spoken of by Professor Wyville Thomson as a proper "vessel;" but, as I shall show hereafter, although it doubtless represents the vascular ring which surrounds the mouth of Echinoderms generally, it is really an extension of the perivisceral cavity, partly separated from the rest. The oral tentacles are of two kinds, extensile and non-extensile. Of the former there are in the first instance only five, presenting themselves at the intervals between the oral valves; whilst of the latter there are ten, a pair lying within each of those valves. Coincidently with the development of the Radials, however, the first-formed extensile tentacles are carried outwards on diverticula from the oral ring, which thus originate the tentacular canals of the arms; whilst five additional pairs of extensile tentacles are developed between the five pairs of nonextensile, raising the whole number to twenty-five, of which the five first-formed are a little external to the rest. With the development of the second and third Radial plates that of the canal-system of the rays proceeds. The five "azygous" extensile tentacles are gradually carried outwards, by the prolongation of their respective diverticula, to the point of bifurcation of the Ray into Arms; and from these diverticula, which now constitute the tentacular canals of the rays, there arises on either side a series of delicate crescentic leaves, each of them having in connexion with it one extensile and two nonextensile tentacles<sup>2</sup>; an arrangement which afterwards comes to be repeated along the arms when they are developed at the bifurcation of the rays, and subsequently along the pinnules which fringe the arms of the adult. Beneath the tentacular canal a tubular extension of the perivisceral space passes along the ventral surface of each ray; and although this appears to form but a single canal, I shall hereafter show that it is very early divided by a horizontal partition extended from the membranous bands that suspend the digestive cavity in the perivisceral space; and that whilst the canal above the partition communicates with the portion of the perivisceral space which lies immediately round the mouth, the canal beneath the partition is extended from the portion of the perivisceral space which occupies the hollow of the calyx. The former I shall term the subtentacular, and the latter the caliac canal; their relations will be found very remarkable.—The general aspect of the young Pentacrinoid, as seen with its tentacular apparatus retracted in a spirit-specimen, is shown in Plate XXXIX. fig. 1, A, for the sake of comparison with the later stages.

61. For some little time after the appearance of the arms, the relations of the skeleton of the calyx to the visceral mass it includes undergo but little change (Plate XXXIX. fig. 1, B); the chief difference consisting in the more compact condition it now comes to present, in consequence of the advanced development of its component pieces. The five basals (Plate XLI. fig. 1, b, b) now possess a regularly trapezoidal form; the

<sup>1</sup> Philosophical Transactions, 1865, Plate XXVI. fig. 3.

<sup>&</sup>lt;sup>2</sup> Ibid. Plate XXVII. fig. 3.

lower part of each being an acute-angled triangle with its apex pointing downwards, and its upper part an obtuse-angled triangle with its apex directed upwards. The sides of the lower triangle are bordered by a somewhat thickened edge of solid transparent calcareous substance, the presence of which marks that the plate has received its full increase in that direction. The adjacent borders of these plates, however, do not come into absolute contact, a thin lamina of sarcode being interposed between them; and there is also a passage left at the truncated apex of the inverted pyramid formed by their junction, through which the axial sarcodic cord of the stem is continued into the calyx. The upper margins of the basal plates have no distinct border, and seem to be still in process of growth. The first radials  $(r^1, r^1)$  now form (with the anal, a, intercalated between two of them) a nearly complete circle, resting on the basals, and separating them entirely from the orals. Their shape is somewhat quadrangular; two of their angles pointing vertically upwards and downwards, and the other two laterally towards each other. Their lower angles are received between the upper angles of the basals; whilst on their upper, which are somewhat truncated, the narrow second radials  $(r^2, r^2)$ are superimposed. Considerable spaces still exist between the adjacent radial plates, except where the anal plate is intercalated in the series; and these are filled only by sarcodic substance. The central portion of these first radials is thickened by the endogenous extension of the calcareous reticulation; and this extends towards its upper angle, so as to form a kind of articular surface for the support of the second radials; but it does not extend over the lateral or alar expansions of these plates, which still retain their original condition of cribriform films. The second radials (r2, r2) differ completely from the first in shape, being rather rods than plates; but they are deeply grooved on their oral aspect, that which is subsequently to become a central canal being not yet closed in. The calcareous reticulation of their outer or aboral surface is cribriform; but the ingrowth from which they derive their solidity is produced, as Professor WYVILLE THOMSON has shown (p. 541), by the development of fasciculated tissue analogous to that of which the stem-joints are composed. The same general description applies also to the third or axillary radials (r3, r3), which, like the preceding, are nearly cylindrical at their proximal extremities, but expand towards their distal ends, so that each presents two articular surfaces, on which are imposed the pair of first brachials.— The oral plates (o, o), which alternate with the second radials, though somewhat internal to them, now present somewhat of a triangular form, their apices pointing upwards; their basal angles, however, are cut off (as it were) by the encroachment of the first radials. At no part of their contour have these plates any definite margin like that which borders the two lower sides of the basal plates; but the calcareous reticulation of which they are composed is continued into the layer of condensed sarcode with which they are invested. Although the form of these plates is generally triangular, yet their surface is not that of either a plane or a spherical triangle, but presents a remarkable unevenness. Near the apex of each there is a deep depression externally, and a corresponding projection internally; and the effect of this projection seems to be that, when

the apices of these plates incline to one another, so as to form a five-sided pyramidal cover to the calyx (Plate XXXIX. fig. 2), the plates will close together not merely at their apices and lateral margins, but also at the upper part of their internal surfaces. There is also a broad depression near the base of each plate, so that its lower margin is somewhat everted. The anal plate (a), which is intercalated between two of the first radials, has a tolerably regular circular shape; but it consists of only a single cribriform film, and has no definite border.

- 62. Concurrently with the advance in the development of the Calyx, the Stem undergoes an increase both in the number and in the length of its component segments; and while it also increases to some extent in its diameter, its solidity is still more augmented by the endogenous growth of its calcareous skeleton. The cribriform plate on which it rests augments both in diameter and in thickness, absorbing into itself (as it were) nearly the whole of the organic substance of the basal disk. Its typical form may be considered as circular; but its margin is usually more or less deeply divided into lobes (Plate XXXIX. fig. 1). Its diameter is usually about 015 inch. In its centre is a deep depression that lodges the end of the lowest joint of the stem .- It will be remembered that the development of each of the original segments of the Stem was shown by Professor WYVILLE Thomson to commence by the solidification of a ring, which occupies what will afterwards become the middle of its length; and that from each of the two surfaces of this ring a hollow cylinder of calcareous trellis-work gradually extends itself. The length of each of these original joints is augmented by new calcareous deposit at its extremities, which finally become compactly rounded off and well defined, so that the apposed surfaces of two segments are clearly marked out from each other, instead of having their irregularities commingled, as in the earlier period of their formation. The diameter of each segment increases by new calcareous deposit on its cylindrical surface, bringing up its whole length to the size of the first-formed median ring, and finally giving to its extremities a slight excess beyond this. At the same time the solidity of each segment is increased by an inward extension of the calcareous trellis-work, which progressively fills up what was at first a hollow cylinder. This internal solidification, however, goes on more slowly than the completion of the external form and dimensions of the segments; for these may present their mature aspect, or nearly so, whilst possessing so little substance that their shape is altered, by the drying up of the soft sarcode-axis of their interior, to that represented in Plate XLI. fig. 4.
- 63. While the original segments, which are stated by Professor Wyville Thomson to be eight in number, are thus advancing towards completion, new segments are being developed in the interval between the highest of these and the base of the calyx. None of my specimens in the stage now described present fewer than twelve segments; so that four at least must have been thus interpolated. That the upper end of the Stem is the part at which the new segments originate, is very plainly indicated by several considerations. It is there that, during the period in which the stem is continuing to increase, we always find the most rudimentary segments; and we may trace, as we

descend the stem, a gradual passage from such as consist of little else than the primordial ring, to those which have attained their complete cylindrical form and their full dimensions. Moreover it is obviously there that the nutritive activity will be the greatest; the sarcode-substance intervening between the base of the calyx and the summit of the stem being in most direct relation with that of the interior of the calvx (through the imperfect closure of its basal plates, § 61), and consequently with the visceral apparatus. And there is no other part of the stem in which there is the least appearance of any multiplication of segments, either by the subdivision of those already formed, or by the interpolation of new ones;—the suggestion of Professor Allman, that the transverse ridges running round the centres of the segments may be the indication of such a division, being negatived by the facts already stated as to its real character. That this ridge, which is prominent in the segments of the upper and middle part of the stem, so far disappears in those of the lower as to be represented only by a single line, is due to the circumstance that the lower segments are those of which the skeleton is first completed.—By the time that the opening-out of the Calyx commences in the manner to be presently described, the number of segments in the stem has usually risen to 15 or 16; those of the inferior third of the stem are pretty nearly solidified throughout, only a small passage still existing through their interior; but those of the middle and upper thirds of the stem are still so far from having attained their completion, that their calcareous cylinders when broken across are found to be mere shells. The highest plate, on which the base of the calyx rests, is now distinguished from those below it by its somewhat larger diameter; but it does not as yet present any approach to the peculiar shape which it afterwards comes to possess.—The entire stem remains clothed with a thin layer of sarcodic substance; and its cavity is occupied by a cylinder of the same, which forms a continuous axis throughout its entire length, and passes up at its summit into the calyx. I have not been able to see any traces, at this early stage, of that fibrous structure which may be distinguished about the ends of the segments at a subsequent time.

64. A very important change now takes place in the relations of the several parts of the Calyx and its contents, which gives to the body of the more advanced Pentacrinoid a much closer resemblance to that of the adult Antedon. For instead of being completely included within a calcareous easing, which not only supports it below, but can close over it above, the visceral apparatus which occupies the cavity of the calyx is henceforth to be merely supported by its skeleton; its upper surface losing all protection except such as is afforded by the infolding of the arms, and being extended into a disk of which the mouth only occupies the centre. This change is essentially connected with the increased development of the intestinal tube, which now forms a nearly complete circle around the stomach, and comes to possess a second or anal orifice. When we examine the composition of the calyx (Plate XXXIX. fig. 1, c, and fig. 3), we find that the original busuls have undergone little if any increase, but that the first radials (r<sup>1</sup>, r<sup>1</sup>) are now much larger, and spread out so as to extend the base of the cup, instead of merely forming

its sides. This spreading-out results from the increase in their own breadth, without a corresponding increase in the diameter of the circle on which they rest; so that they are forced to extend themselves obliquely instead of vertically. The single anal plate (fig. 3, a), originally interposed between two of the first radials  $(r^1, r^1)$ , being attached not so much to the neighbouring plates as to the visceral mass, begins to be lifted out (as it were) from between them with the development of the anal funnel, as is seen in Plate XL. fig. 2; and the space left by it is partly filled up by the lateral extension of the two radials between which it was previously interposed, but which do not yet come into mutual contact. The second and third radials  $(r^2, r^2, and r^3, r^3)$  also increase in all their dimensions, but particularly in breadth; and they thus assist in supporting the visceral mass, which, at the conclusion of this stage, extends itself as far as the bifurcation of the arms. The most remarkable change in the condition of the calcareous skeleton in this stage, however, consists in the altered relative position of the five oral plates (Plate XL. fig. 1, o, o). This circlet, like that of the basal plates, does not partake of the enlargement so remarkably seen in the radials; its diameter being neither increased by the growth of its component plates, nor augmented by their separation from one another. It continues to embrace the circle of oral tentacles, the diameter of which comes to bear a smaller and yet smaller proportion to that of the ventral surface of the disk, as the size of the latter is augmented by the development of the intestinal tube around the gastric cavity; and thus it comes to pass that the circlet of oral plates detaches itself from the summits of the first radials on which it was previously superimposed, and is relatively carried inwards by the great enlargement of the circle formed by the latter,—the space between the two series being now filled in only by the membranous perisome, which is traversed by the five radial canals that pass out from the oral ring between the oral valves to the bifurcation of the arms, as shown in Plate XL. fig. 1.

65. In the earlier part of this stage, a continued increase takes place in the number of segments of the Stem, by the development of new rings at its summit; whilst the previously-formed segments of its middle and upper portions become progressively elongated and solidified, as those of the lower portion have previously been. At or about the period, however, at which the change already described is taking place in the relations of the oral and anal plates of the Calyx, the production of new calcareous segments in the stem appears to cease; and a remarkable change begins to show itself in the one on which the calyx rests. Instead of increasing in length, its original annular disk augments in diameter, becoming convex on its lower surface, and concave on its upper; and it extends itself over the bottom of the calyx, in such a manner as to receive into its concavity the apices of the basal plates. This change commences whilst the calcareous segments next below are still rudimentary; so that although no further increase in the number of segments takes place subsequently, yet some increase in its length will still be effected by the completion of the last-formed segments, previously immature. The total number of segments in the fully-developed Pentacrinoid stem is subject to a

good deal of variation. I have counted as many as 24, and as few as 16; the average may be considered about 20.

66. Soon after the highest segment of the Stem begins to enlarge, we notice on that portion of its under surface which extends itself beyond the segment whereon it rests, one or more minute tubercles, which are the origins of the dorsal cirrhi. Each of these tubercles is formed by a projection of the sarcodic substance of the perisone, within which are observable one or more minute annular disks of calcareous reticulation. The projection of the tubercle gradually increases, and the number of disks (which are the rudimental segments of the dorsal cirrhi) is multiplied; so that each incipient cirrhus presents the form of a short cylinder marked by transverse annulations (Plate XI. figs. 1, 2, cir). The length of this cylinder is progressively augmented by the formation of new disks, and by an increase in the thickness of the earlier ones; and the terminal segment soon presents an indication of the peculiar character it is ultimately to assume. Hence it is obvious that the new segments cannot be added at the extremity of the tentacle; and since, during the whole progress of its growth, we always find that the basal segment is the shortest, it seems most probable that the increase in the number of segments is effected by the interpolation of new segments at the point at which the cirrhus springs from the plate which bears it,—a conclusion which is conformable to what has been already stated (§ 29) of the relation of the cirrhi to the peculiar modification of the central axis contained within the centro-dorsal basin.—As each cirrhus clongates itself, its extremity, which was at first bluntly rounded, becomes pointed, the terminal segment developing itself into a conical form, though still covered with the same thick investment of condensed sarcode as extends over the entire length of the rudimentary cirrhus. —The exactness with which radial symmetry is maintained throughout the formation of the skeleton of this organism (save in the case of the Anal plate, which has special reference to the visceral mass), would lead us to anticipate that the first five cirrhi would be put forth together, radiating from the central tubercle, and developing themselves at corresponding rates. This, however, is not the case, for they are developed successionally, the first of them usually exhibiting numerous segments with a conical termination by the time that the fifth makes its appearance (Plate XXXIX. fig. 1, D). The cirrhi of the first whorl alternate in position with the rays, so that one of them is opposite to the anal plate; and this I generally (though not always) find to be the latest in its development, the most advanced being the one which corresponds in position to the commencement of the intestine.

67. The development of the Arms continues to take place on the plan already described in detail by Professor Wyville Thomson. Each of them is terminated by a "growing point" of condensed sarcode, in which new segments successionally originate (Plate XXXVIII. fig. 1), a cribriform calcareous film being first formed on the dorsal face, and an ingrowth of fasciculated calcareous tissue then taking place in such a manner as in the first instance to leave a deep groove on the ventral face, which is afterwards converted into a canal by the closing-over of its margins; so that the transverse section which at first

resembles a horseshoe finally comes to be a ring. I feel quite satisfied that there is no interpolation of new segments (as some have supposed) either at the base or at any part of the length of the arms, their longitudinal growth being effected in part by the addition of new segments to their extremities, and in part by the augmentation in the length of each individual segment. Thus the average length of the basal segments of the arms in this stage of Pentacrinoid life is about '007 inch, and their diameter about '003 inch; whilst in the adult Antedon their length averages about '03 inch, and their diameter about '07. As the skeleton of the arms increases in length, their vascular apparatus is prolonged, and new groups of tentacles are developed from its extensions, each of these consisting, as before, of a leaf-like expansion with three tentacles proceeding from its base, of which one is much more extensile than the other two. The sarcodic substance which unites the pieces of the skeleton now begins to show a delicate fibrous texture at their adjacent extremities; but no separate fibres are as yet to be distinguished.

68. The changes which we observe during the later stages of Pentacrinoid life (Plate XXXIX. fig. 1, p, e) form in every respect a continuation of those already described. The Calyx is still more opened out by the increased lateral as well as longitudinal development of the first radials; but the diameter of the visceral disk augments in even larger proportion, so that it extends nearly as far as the bifurcation of the arms. The oral circlet is thus separated by a much wider interval from the periphery of the disk; and in this outer ring the anal funnel (Plate XL. fig. 2, v) is now a very conspicuous object, the anal plate (a) which it bears on its outer side being altogether lifted out from between the two first radials which it originally separated. Before the body of the Pentacrinoid drops off its stem, an incipient absorption of the oral plates is discernible; this absorption commencing along the margins of the apical portion, so that these plates lose their triangular form and become somewhat spear-shaped. The second and third radials exhibit an increase in all their dimensions, without much departure from their original form.

69. The Arms continue to increase in length, both by the addition of new segments, and by the growth of those previously formed; and it is when they have attained the length of about '08 inch, and consist of about twelve segments, that we see the first indication of the development of pinnæ. This shows itself, not (as might have been expected) at the base or oldest part of the arm, but at its growing extremity, which now presents a bifurcation (Plate XL. fig. 1), the two rami being in the first instance almost equal, and each tumefied at its extremity by an accumulation of sarcode-substance. One of these rami, however, grows faster than the other, and soon takes a line continuous with that of the axis of the arm, from which the other diverges at an acute angle; so that the former comes to be the proper extension of the Arm, whilst the latter soon takes on the characters of a Pinnule. Ere long, however, the growing point of the arm again subdivides; two branches are formed, as previously; and whilst one of these becomes a continuation of the arm, the other is soon to be distinguished as a pinnule

given off from it on the side opposite to that of the first-formed pinnule. Thus the formation of the first pair of pinnules takes place in such a manner that the extremity of the arm presents an appearance in the first instance of bifurcation, and then of trifurcation. The new segments henceforth added to the extremities of the arms are all pinnated; the pinnules (whose skeleton consists, in this stage, of six or eight simple cylindrical segments) being developed alternately from one side and the other, and being furnished with extensions of the tentaculiferous apparatus of the arms. Owing to the thickness and opacity of the cumulus of condensed sarcode in which they originate, I am not able to speak with positiveness as to the mode of formation of their calcareous skeleton; but I believe it to take place rather after the manner of the joints of the stem and dorsal cirrhi than after that of the segments of the rays and arms,—that is, to commence with a complete ring which extends itself longitudinally into a hollow cylinder, rather than by a cribriform plate which wraps itself (so to speak) around the extension of the sarcodic axis (§ 67). It is remarkable that the basal portions of the arms, which had been developed previously to the first appearance of the terminal pinnules, remain destitute of these appendages to the end of the Pentacrinoid stage; except in the case of the second segment, from which, on each arm, an oral pinnule (§ 54) is developed.—The connexion of the segments of the arms by distinct fibrous tissue is now clearly discernible; but this tissue corresponds rather with the ligamentous than with the muscular tissue of the adult Antedon.

70. The Stem, in this later stage of Pentacrinoid life, shows no increase in the number of its segments; but those last formed near its summit are developed to almost the same length as the rest; and all the segments are somewhat augmented in diameter towards their extremities, so as to present somewhat of the dice-box form. The original annulus, which is still distinguishable in the middle of their length, so far from constituting a projection, now lies in a hollow. The axial cavity, if not quite obliterated by the filling up of the segments, is very much contracted; on this point it is difficult to arrive at a positive determination. The connexion of the segments by a distinct fibrous tissue, resembling that of the arms, and not merely passing from one articular extremity to the other but also embracing the contiguous extremities which it connects, now becomes obvious.—The most important change which the stem presents at this period consists in the enlargement of its highest basin-shaped segment, from which the dorsal cirrhi are developed, and in the further development and multiplication of the cirrhi themselves. This segment, which now presents the aspect in miniature of the centro-dorsal plate of the adult Antedon, augments not only in absolute but in relative diameter, extending itself over the dorsal or outer surface of the basal plates, which, at the time of the detachment of the body from the stem, are almost entirely concealed by it. The first-formed whorl of cirrhi now shows itself ready for prehensile action, its terminal claws being hooked, the calcareous segments being bevelled off on their dorsal aspect so as to allow of the downward flexure of the cirrhi, and a considerable amount of contractile fibrous structure being developed between and around the extremities of the segments. A second 5 н MDCCCLXVI.

whorl of cirrhi is now developed after the same manner as the first, between the latter (with which it alternates in position) and the base of the calyx (Plate XLII. fig. 3); and a third whorl generally makes its appearance before the detachment of the Pentacrinoid, so that the young Antedon possesses ten cirrhi in different stages of advanced development, and from one to five still rudimentary.

- 71. The total length of the full-grown Pentacrinoid, from the base of the Stem to the extremities of the Arms when these are folded together, may be about ·7 inch, that of the stem alone being about ·25 inch; when, on the other hand, the arms are fully expanded radially, the diameter of their circle may be about ·5 inch. At this period the body and arms usually possess a decided colour, which is sometimes sulphur-yellow, sometimes light crimson, sometimes an intermixture of both hues; this is usually more pronounced in the arms than in the body, and is entirely due to the development of pigmentary matter in the minute pyriform vesicles scattered through the sarcodic layer which still forms, as in the earliest phase of embryonic life¹, the general envelope of the body and its appendages.
- 72. The precise stage of development at which the body of the animal becomes detached from the stem, varies, like that at which a ripening fruit drops off its stalk, according to circumstances. I have met with specimens still attached to their stems, which were larger and more highly coloured than others which were found free; and I have repeatedly noticed that when kept in captivity they fall off quite spontaneously at an earlier period than that at which they detach themselves under ordinary circumstances. But the detachment does not seem to take place normally, until the dorsal cirrhi are sufficiently developed to enable them to take the place of the stem functionally by giving the animal the means of attaching itself to fixed objects.
- 73. Habits.—Concerning the habits of the Pentacrinoid I have little to add to what has been already noticed by Mr. J. V. Thompson<sup>2</sup>. "The animal," he says, "possesses the power of bending or inclining the stem freely in every direction; and what is more remarkable, of twisting it up into a short spiral, and that, with a considerable degree of vivacity,—a kind of movement that has not been noticed except in the Vorticellæ." He speaks of the arms as "at one time spreading outwards like the petals of a flower, at another, rolled inwards like an expanding bud;" and continues,—"From their structure and movements it can hardly be doubted that they serve to seize upon and convey to the mouth whatever has been destined for its food, and which probably consists in every minute animal its powers enable it to overcome." Now, whilst I am quite at one with this excellent observer as to the facts which he records, I differ from him in regard to their interpretation; for I have seen nothing to make me believe that in the Pentacrinoid, any more than in the adult Antedon, are the arms ever employed for prehension; whilst the existence of large vibratile cilia on the walls of the digestive cavity, as seen by Professor Wyyille Thomson in the early Pentacrinoid, and by myself in the more

<sup>&</sup>lt;sup>1</sup> See Professor Wyville Thomson's Memoir, Philosophical Transactions, 1865, pp. 522, 535.

<sup>&</sup>lt;sup>2</sup> Memoir on the Pentacrinus Europæus, p. 7.

advanced, as well as in the adult Antedon, sufficiently accounts for the ingestion of alimentary particles, without attributing to the arms any prehensile action. Neither the oral nor the brachial tentacles are ciliated; but I have frequently noticed a rapid movement of particles along the radial furrows and their brachial extensions, which intervene between the parallel rows of leaflets and tentacles developed on either side of the tentacular canals, such as indicates the action of cilia along the floor of those furrows. And as this movement always takes place from the extremities of the arms towards the mouth, I feel little doubt that it serves the purpose of bringing within reach of the ingestive current maintained by the gastric and intestinal cilia such alimentary corpuscles as settle down upon the expanded arms and pinnules.

# 2. Development of the Component Pieces of the Skeleton, from the commencement of the free or unattached stage.

74. Having thus traced the history of the Pentacrinoid Larva to the stage at which it assumes its adult condition as a free *Antedon*, I shall describe in some detail the several pieces of which its skeleton is then composed; and shall then trace the further development of each to its final completion.

75. Beginning from the base, we have first to speak of the Centro-dorsal plate, or rather basin; which, as was rightly stated by Professor J. MÜLLER, is really the highest joint of the Pentacrinoid stem; whilst, as pointed out by Professor Wyville Thomson2, "it represents a coalesced series of the nodal stem-joints in the stalked Crinoids." Of this sagacious determination I shall hereafter (Part II.) adduce a most curious and unexpected confirmation. The centro-dorsal plate (Plate XLI. fig 2, c) at the stage now treated of, has the form of a basin with its lip inverted instead of everted; its diameter is about 03 inch, and its height about 012 inch. Its basal surface is somewhat depressed in the centre; and here we may for a time distinguish a minute fiverayed perforation (fig. 6, c), which previously formed the communication between the cavity of the basin and the central canal that is still left in the upper segments (at least) of the stem. This perforation, however, is very soon closed up by an extension of the calcareous network, so that no trace of it remains visible either externally or internally. Around the stellate aperture is seen a circular series of five sockets for the articulation of the dorsal cirrhi, each of them having a pore in its centre, which is usually at the summit of a minute elevation. This pore gives passage to a sarcodic thread which proceeds from the sarcodic axis contained within the cavity of the basin, and runs along the central canal of the cirrhus to its termination. A second series of sockets, alternating in position with the first, is seen nearer the upper margin of the basin. This margin,

<sup>&</sup>lt;sup>1</sup> Mr. J. V. Thomson speaks of the brachial tentacula as "furnished with capitate cilia, alternately placed along their sides;" but it is clear that he referred to the tubular processes of the tentacles which have been described by Professor Wyville Thomson (p. 526), and that, writing in 1827, he did not employ the term *cilia* in the technical sense to which it is now limited, but merely meant distinct hair-like filaments.

<sup>&</sup>lt;sup>2</sup> Philosophical Transactions, 1865, p. 536.

when viewed from above, is somewhat pentagonal; but the opening left by the inversion of the lip is nearly circular. Looking down into its cavity, we may distinguish what was once the central canal (now blocked up), and the pores leading to the articulations of the cirrhi.

76. The circlet, or rather pentagon, of Basal plates (Plate XLI, figs. 5, 6, b, b), which is for the most part concealed externally by the centro-dorsal basin, is found, when exposed by the removal of the latter, to differ very little either in size or aspect from the circlet first completed in the Pentacrinoid (§ 59). The form of each plate (Plate XLI. fig. 2, B) is an irregular trapezoid, with its lower angle truncated; and it still retains the solid pellucid margin which originally characterized it. But it has undergone a remarkable thickening by an endogenous extension of its calcareous network; and this has taken place in such a manner as to leave its substance channelled out by a canal which commences at its lower truncated angle, and almost immediately bifurcates, the two branches diverging in such a manner as to pass towards the two First Radials which severally abut on the sides of the upper triangle of each basal (Plate XLII, figs. 6, 7). This canal gives passage to a large sarcodic cord that proceeds from the wall of a remarkable quinquelocular organ contained within the centro-dorsal basin, which I shall hereafter describe under the name of the "centro-dorsal vesicle," and which I shall show to be an expansion of the original Crinoidal axis, hollowed out into a multiple ventricular cavity. Each of the five primary cords (which originally lay on the internal surface of the basals forming the floor of the calyx) subdivides into two branches within the basal whose canal it enters; and thus each of the First Radials receives two branches supplied to it through the two basals whereon it rests.

77. The form of the First Radials (Plate XLI. fig. 2, R1, fig. 5, r1, and XLII. figs. 5, 6,  $r^1$ ,  $r^1$ ) is now that of a trapezium having its upper and lower sides nearly straight and parallel, whilst its lateral margins incline towards each other from above downwards. Externally they still present their original cribriform structure; and this is particularly obvious near the upper angles, where the first-formed perforated plate has not been thickened by internal addition. But whilst the external surface is convex, being arched from side to side, the internal is nearly plane, the concavity of the cribriform plate being filled up by an ingrowth of its calcareous reticulation, which still retains for the most part its original type. This ingrowth, however, takes place in such a manner as to leave two deep channels, which commence from the lower angles of the plate, and converge so as to meet in its centre, so as to form one large canal, which becomes completely covered in and passes to the upper margin of the plate, where it opens between the articular surfaces. These converging channels, when the plates are in situ, are continuous with the diverging canals of the two Basals whereon each Radial abuts; in such a manner that the primitive canal that enters each basal communicates by its bifurcation with the converging canals of two different radials; while the single canal of each radial is fed (so to speak) by the primitive canal of two different basals. At each of the lower angles of the radial, moreover, the wide embouchure of the converging channel is in proximity with that of its

adjacent radial (Plate XLI. fig. 5); and a continuity is thus established between the several parts of this canal-system, not only radially but peripherally. At the somewhat later period represented in Plate XLII. figs. 6, 7, the channels are completely covered in, so as to be converted into canals; and each embouchure is divided by a small calcareous islet into two passages, one of them opening opposite the canal of the basal, and the other opposite the corresponding canal of the adjacent radial. In this manner are formed the canals already described in the first radials of the adult Antedon (§ 34). The upper margin of the first radial now shows on either side of its centre an elevated articular surface (Plate XLI. fig. 2,  $\mathbb{R}^1$ , a, a), the calcareous reticulation of which is much closer than that of the rest of the plate; and each of these gives attachment along its dorsal border to a distinctly fibrous ligament connecting it with the corresponding articular surface of the Second Radials; whilst from the ridges which form its ventral border there are now seen to pass towards the opposite face of the second radials a set of larger and more defined parallel fibres, which, from their similarity to those occupying the like position in the adult, we know to be muscular.

78. The Second Radials (Plate XLI. fig. 2,  $\mathbb{R}^2$ ) now begin to show a modification of their original nearly cylindrical form; being somewhat widened out at their lower end, so as to form two articular surfaces (a, a), which are not, however, directly opposite to those of the first radials, but slope away from them; so that whilst in close proximity with them on the dorsal face, where they are connected by ligament, they are separated by a considerable interval on the ventral side where muscle intervenes,—an arrangement which gives to the muscular fibres the length required for their efficient contraction. The upper end (b) of the second radial, however, is simply rounded off, presenting no proper articular surface; and it is connected with the base of the Third Radial by ligament only. Although the dorsal surface of the second radial is everywhere convex, its ventral face still shows a deep groove along its median line; this, however, is separated by a distinct layer of calcareous network from the axial canal beneath it, which opens at its lower end between the articular surfaces, and at its upper in the centre of the rounded termination.

79. The Third or Axillary Radials (Plate XLI. fig. 2, R³) also show but a slight departure from the original simple type; their lower portion being incompletely cylindrical, whilst the upper is somewhat expanded laterally to form a pair of articular surfaces, which look obliquely towards either side, and are separated by a projecting median ridge. The lower extremity is rounded off, so as to resemble the upper end of the Second Radial, and shows, like it, the orifice of the axial canal in its centre; whilst each of the articular surfaces at its upper end shows a similar perforation, which is the orifice of one of the two branches into which the axial canal bifurcates in the interior of the segment, for the supply of the two Arms borne by it. The dorsal face of this segment is everywhere irregularly convex; but the ventral face has a deep depression in its centre, the bottom of which almost reaches the axial canal.

80. The segments which form the skeleton of the Arms (Plate XLII. fig. 5) at this

period, depart even less than the preceding from the simple type of conformation which they present at their first development (§ 67), being still obviously composed of the original cribriform plate, which constitutes their convex dorsal surface, with an ingrowth of fasciculated tissue that closes over the axial canal, and gives to the ventral aspect a flattened surface with a median groove. This ingrowth is most abundant towards the extremities, where also the meshes of the reticulation are smaller, so that these parts have a more solid character than the rest. We now begin to see that alternate inclination to one side and the other, which is so marked a feature in the articular extremities of the segments of the adult; and we also notice that whilst these extremities are in close contact with one another on the dorsal aspect (B), except where a small depression exists in each for the attachment of the articular ligament, the articular surfaces of the ventral face (A) slope away from each other so as to leave a considerable space for the lodgment of the two muscular bundles, which are now conspicuously interposed between each pair of segments in the basal part of the arms, with certain exceptions. These exceptions correspond with those which present themselves in the adult ( $\delta\delta$  47–50); though the peculiarities of conformation which mark them are as yet but little pronounced. Thus the adjacent extremities of the first and second brachial segments present nearly the same aspect on their ventral as on their dorsal face, no bevelling-off being seen on the articular surfaces of either; and they are connected by ligament only, no muscular fibres being here distinguishable. Again, the adjacent articular surfaces of the third and fourth segments come into yet closer contact, not even a connecting ligament being interposed, and the line of their junction being transverse instead of oblique; this prefigures the peculiar syzygal union which shows itself between these and other pairs of segments in the adult (§ 50).—Towards the extremities of the Arms, we find the segments even more cylindrical (Plate XLI, fig. 4, A, B), except where lateral processes are given off for the articulation of the pinnules; and their terminal faces are simply apposed to each other transversely, without either the alternate obliquity or the bevelled articular surfaces of the basal segments. And at the growing points of the Arms precisely the same rudimental condition of the segments presents itself (Plate XXXVIII. fig. 1), as that which has been already described (§ 67) as showing itself at an earlier period in their basal segments. Thus we may trace in one and the same Arm several successive stages of development of the pieces of its skeleton; the most advanced segments (those nearest the base of the arms) showing adumbrations of their adult peculiarities, although not yet departing in any considerable degree from their simple primitive type.

81. Besides the regular skeleton of the Arms, we commonly find their perisome of condensed sarcode to contain irregular branching spicules (Plate XLII. fig. 5, A, B), forming a sort of incomplete reticulation for the support of the elevated folds which constitute the margins of the ventral furrows. These are obviously the rudiments of the dermal plates which have been shown by Professor J. Müller to form a complete armour to the ventral perisome and its prolongations along the ventral surface of the arms in *Pen*-

<sup>1</sup> Über den Bau des Pentacrinus Caput-Medusæ, p. 48.

tacrinus Caput-Medusæ. It is curious that this perisomatic skeleton of the Arms, like the Oral plates ( $\S\S$  82, 94), subsequently undergoes complete absorption, so that no trace of it is discoverable in the adult Antedon.

82. The only portions of the skeleton of the young Antedon now remaining to be described are the Oral and the Anal plates; and respecting these there is but little to be said. The only change which the five Orals have undergone consists in a further advance of the process of absorption, the commencement of which has been already noticed (§ 68). This process goes on with considerable rapidity during the period at which the pedunculate *Pentaerinoid* is being transmuted into the free *Autedon*; and as the epoch of its detachment from the stem is not always precisely the same ( $\delta$  72), so the amount that has been removed by absorption at that epoch varies in different specimens. In some we find the upper half or even two-thirds of each oral plate to have entirely disappeared; whilst in others the marginal portions only of the upper part of the plate have been removed, leaving a sort of central tongue projecting upwards from the basal portion. The single Anal plate (Plate XLI, fig. 2, A) still retains the elliptical form which characterized it from the time when it was lifted out from the circlet of radials  $(\delta 64)$ ; and it seems to have undergone but little change in any of its dimensions, either by addition or absorption. It is still a simple cribriform film, of which the lower portion shows a closer texture and a more uniform margin than the upper; and it is not connected with any other portion of the skeleton, save by the general perisomatic substance.

83. The entire skeleton of the Calyx—putting aside the centro-dorsal piece as really belonging to the stem—may be described, according to the formula of MM. DE KONINCK and LE Hon (op. cit.), as consisting of the following pieces:—

84. Professor Wyville Thomson, however, regards the skeleton as composed of two systems of plates, the radial, and the perisomatic; which he states to be "thoroughly distinct in their structure and mode of growth". The Radial system consists of the joints of the stem, the centro-dorsal plate, the radial plates, and the segments of the arms and pinnules. The Perisomatic system includes the basal and oral plates, the anal plate, the interradial plates sometimes seen between the second radials (§ 39), and any other plates or spicules that may be developed in the perisome of the disk or arms (§§ 39, 81). Whilst partly agreeing with him on this point, I find myself unable to accept his distinction to its full extent, since its basis is not in harmony with my own observations. "The joints or plates of the radial system," he says, "may be at once distinguished by their being chiefly made up of the peculiar fasciculated (or radial) tissue

<sup>&</sup>lt;sup>1</sup> Philosophical Transactions, 1865, p. 540.

of parallel rods which I have already described, and by their being perforated for the lodgment of a sarcodic axis." The extended researches which I formerly made on the calcareous skeleton of Echinodermata generally, would lead me to attach but little importance to the form of the reticulation as a differential character, since this often varies greatly in the several portions of a single plate; and Professor Wyville Thomson is forced by his reliance upon it to regard the superficial cribriform portions of the radial plates and even of the arm-joints as belonging to the perisonatic system,—a supposition which seems to me inconsistent with the fact that the ingrowth of the calcareous reticulation in the First Radials, by which the axial canal is at first formed as a groove and is afterwards covered in (§ 77), takes place on the cribriform, not on the fasciculated type. In fact there is no distinction in texture between the endogenous additions by which the first radials and the basals are respectively thickened; so that we cannot place them in separate categories on this score. But further, we have seen that in the stage now described, the Basals as well as the Radials are perforated to give passage to the radiating extensions of the sarcodic axis of the stem, which only reach the radials through the basals; so that this ground of distinction also fails to separate them.—I am myself disposed, however, to regard the perforation or non-perforation by the radiating extensions of the Crinoidal axis as quite sufficient in itself to differentiate the entire skeleton into two series of plates, which, with Professor Wyville Thomson, I should term the radial and the perisonatic; but I should rank the Basal plates with the former, instead of with the latter.

85. I shall now describe the changes which each of the component pieces of the skeleton undergoes in its progress towards the type which it presents in the fully-developed Antedon.

86. Centro-dorsal piece..—Through the whole period of growth, the increase of this segment takes place at a greater rate than that of any other part of the skeleton; so that it soon comes to pass beyond the circlet of Basals, and to abut on the proximal edge of the First Radials; and instead of stopping here, it continues to increase in diameter, until it conceals the whole inferior surface of the first radials, and sometimes even encroaches somewhat on the Second (Plate XXXII. fig. 1). When we examine into the conditions of this increase, we find them to bear a remarkable resemblance to those which prevail in the growth of the skeleton of Vertebrated animals. For when we bear in mind the form of the basin, with its cavity and inverted rim (§ 22), and witness its augmentation in size from its original diameter of .005 inch to its final diameter of '16 inch, with a corresponding augmentation of its cavity, it becomes obvious that there must be not merely a progressive deposit of new material on the external surface, but also a continual removal of old material from the internal surface, analogous in every respect to that by which the cavity of a cylindrical bone is enlarged by absorption from within, at the same time as the diameter of its shaft is augmented by the deposit of new layers of bone on its exterior.

<sup>&</sup>lt;sup>1</sup> Reports of the British Association for 1847, p. 117 et seq.

87. With this general augmentation in size, there is an increase both in the number of sockets for the articulation of the Dorsal Cirrhi, and in the size of the individual sockets; and there is also a marked change in their disposition. I have not been able to satisfy myself that after the development of the first two whorls, each consisting of five cirrhi, any similar regularity is observable in their subsequent multiplication; but since, as I shall more fully explain hereafter, the real origin of each cirrhus is in a peduncle of sarcodic substance put forth from the central axis in the cavity of the centro-dorsal basin, and since the arrangement of the whole aggregate of such peduncles is distinctly verticillate, the want of a definite plan in the grouping of the cirrhi on the external surface of that plate seems attributable to their very close apposition. The new cirrhi always make their appearance between those previously formed and the base of the calyx, so that their sockets are close to the margin of the basin; and this is the position in which, as already stated (§ 26), we find those rudimental cirrhi that often present themselves even in the adult Antedon. The increase of the cirrhi in diameter is by no means proportional to the increase in the diameter of the centro-dorsal plate; so that not only is space made on its surface for the augmentation in the number of their sockets from 10 to between 30 and 40, but a vacancy gradually comes to be left in the central part of the exterior of the basin, which extends with its growth, and finally comes to bear a considerable proportion to its diameter (§ 22). This vacancy cannot be accounted for solely by the widening-out of the innermost circle of sockets by the general growth of the basin in the manner already described; and I feel no doubt that it is principally due to a progressive exuviation of the first-formed cirrhi from within outwards, concurrently with the development of new ones near the margin; those cirrhi which surrounded the summit of the stem being first shed, and their sockets being filled up by new deposit; and the space thus formed being gradually widened by the progressive exuviation of the cirrhi that bound it, and the filling-up of their sockets. For in comparing a series of centro-dorsal plates in different stages of development, I find distinct traces of such an obliteration of the original sockets; and when we come to study the connexions of the sarcodic axes of the cirrhi with that central Crinoidal axis, of which the portion not left behind in the Stem is included within the Centro-dorsal plate, we shall find additional evidence to the same effect.—Thus it appears that the total number of dorsal cirrhi developed during the life of any individual Antedon, considerably exceeds that which we meet with at any one epoch. How many of the earlier cirrhi are exuviated before the latest are put forth, I cannot state with certainty; but I should think that the number cannot average less than from 15 to 20, thus raising the total to at least 50.

88. Before leaving the Centro-dorsal basin, there is a further point of much interest to be noticed in regard to its growth; namely, the perforation of its wall for the passage of the new twigs which are given off from the central axis from time to time, and which, when they emerge on its external surface, become the sarcodic axes of the cirrhi. It scarcely seems probable that such perforations should be left as vacuities in the MDCCCLXVI.

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exogenous additions made to the calcareous reticulation, whilst the radiating sarcodic twigs for whose passage they are destined are prevented from gaining access to them by the imperforateness of the inner wall. And looking to the numerous examples which we have in the development of Antedon, not only of the entire absorption of some parts of the skeleton, but of the complete remodelling of others,—as shown in the growth of this very plate, and still more remarkably in the formation of the "rosette" from the original "basals" ( $\delta \delta$  89, 90),—I cannot but regard it as more probable that these cirrhal twigs, as they are successively put forth in the cavity of the basin and impinge upon its inner wall, have the power of forcing (as to speak) a passage for themselves, by inducing an absorbent action in that part of its substance that lies in their course towards the external surface.

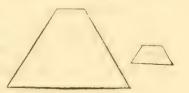
89. Basal Plates.—The mode in which the "rosette" (§ 35) is formed by the remodelling and subsequent coalescence of the five Basals, and in which the sarcodic extensions of the central axis which are transmitted through the Radial plates to the Arms and pinnules, come to lie on the dorsal or external face of the "rosette," whilst they originally lay along the ventral or internal face of the basals, is certainly the most curious feature in the developmental history of the skeleton of Antedon.—It has been already shown ( $\sqrt[6]{76}$ ) that the cribriform plate of which each basal at first entirely consisted, is so much thickened by endogenous growth during the later stages of Pentacrinoid life, that the radial sarcodic cords come to be entirely invested by calcareous reticulation; and the floor of the ventral cavity shows no inequality as we pass from the central portion formed by the basals to the peripheral formed by the radials (Plate XLI. fig. 5). Very soon after the detachment of the young Antedon, however, a remarkable change begins to show itself in the basal pentagon, which is now entirely concealed externally by the extension of the centro-dorsal basin over its dorsal surface; for the cribriform film of which each basal plate was originally composed, and which still forms its external layer, now undergoes absorption, especially where it covers in the radial prolongation of the axis, so that the central space left by the incomplete meeting of the valves of the basal pentagon, is extended on its external aspect into five broad rays (Plate XLII. fig. 7, b), though on its internal or ventral aspect, where it is bounded by the last-formed portion of the endogenous reticulation, it shows no corresponding increase (Plate XLII. figs. 2, 6, b).

90. This removal of the older and outer part of each basal plate by absorption, and the consolidation of the newer and inner by additional calcareous deposit, go on at a rapid rate; so that in specimens whose size and general development show but little advance upon the earliest Antedon type, we find the basals already modelled into such a form that their coalescence will produce a somewhat unshapely "rosette." In Plate XLI. fig. 3, a, is shown the dorsal aspect of one of the basal plates in which the removal of the external layer has been carried so much further, that what is now left of it constitutes only a kind of thickened margin along those sides of the plate which are received between the First Radials; and by an extension of the same process along the median

line of each plate, until the external layer has been completely removed from its salient angle (fig. 3, b), the two lateral portions of that layer are separated from each other; and remain only as a pair of curved processes extending themselves from the inner layer in such a manner as to give to the plate when viewed from its ventral side somewhat the aspect of a saddle (fig. 3, c, d). When the five Basals thus altered are in their normal apposition, the curved process on either side each plate comes into contact with the corresponding process of its next neighbour; and the junction of the two forms a sort of ray curving towards the dorsal aspect. As each plate thus contributes the half of two of these curved rays, five such rays are formed between the five salient processes which are put forth by the internal or ventral layer, on the median lines of the five plates, and are received into the retreating angles formed by the junction of the First Radials. Very soon an actual continuity is established in the calcareous reticulation along the lines of junction, and the "rosette" is completed, as shown in Plate XLII. fig. 1, although the peculiarity of its shape becomes much more strongly pronounced with the subsequent increase of its size (Plate XXXIII, figs. 9-11).—Thus we see that the "Rosette" is essentially formed at the expense of the secondary or ventral layer of the original Basals, the ends of the curved rays being the sole residue of their primary or dorsal layer; and since, by the removal of the median portion of that layer in each plate, the radial cords are left bare on their dorsal aspect, they now pass from the central axis into the canals of the First Radials on the outside of the calcareous skeleton which occupies the central part of the base of the Calyx, instead of reaching these by passing (as they did in the first instance) along its internal face, or (as at a later period) through the middle of its substance.

91. First Radials.—In the passage of these plates from their rudimental to their mature condition, the principal alteration that we notice, besides an immense increase in size, consists in a change in the proportions of their principal dimensions, their thickness and solidity increasing much more rapidly than their superficial extension. This increase takes place in such a manner that the lateral portions of the plate are brought to the same thickness with the median, the dorsal and ventral surfaces becoming nearly parallel; and the lateral faces come to be flattened against each other, and to adhere so closely that by the apposition of the five plates a solid annulus is formed. The diameter of the central space of this annulus, which is occupied by the "rosette," does not increase during growth in nearly the same degree as that of its periphery, the size of each plate (it would seem) being more augmented by addition to its external face than to its lateral faces; so that the ratio of its breadth at its inner and its outer margins, instead of being (as at the conclusion of Pentacrinoid life) about 2:3, comes to be only 1:3, the shape

of its dorsal face being thus changed from a trapezoid to a triangle with its apex truncated. Concurrently with these changes, we find that the various ridges and fossæ on the external and ventral faces of the plate (§ 33, Plate XXXVI. fig. 1, A, c), for the attachment of the muscles and



ligaments by which it is articulated to the Second Radial, are gradually developed into the form they present in the adult; and that the characteristic ridges and furrows of its internal face (B), with the prolongations that connect it with the ventral face of the rosette, make their appearance. All these features are marked out when the size of the plate is still minute as compared with that which it ultimately attains; and a little consideration will show that they cannot be maintained through each subsequent stage of growth, without a process of modelling analogous to that already described in the growth of the centro-dorsal and basal plates,—the first-formed portions of the calcareous skeleton being removed by absorption, whilst new deposits are being laid down elsewhere. If any further evidence of this be needed, it will be found in the enlargement of the Canals which are occupied by the radial prolongations of the central sarcodic axis, the diameter of these canals in the adult being at least equal to the whole breadth of the plate in the young.

92. Second Radials.—The alteration which the form of the Second Radials undergoes in their progress to maturity, is even greater than that of the First; for whilst they increase but little in the direction of their original length—i. e. in the space between their proximal and their distal faces,—they undergo a great augmentation both in breadth and in depth (Plate XXXVI. fig. 2), their proximal face attaining an equality in both dimensions with the distal face of the first radial to which it is articulated, and its distal face coming to present a similarly expanded surface to the proximal face of the third radial, in the place of the mere convexity in which the then cylindroid segment terminated at an early period (§ 78). This change in the proportion of the several dimensions of these plates begins to show itself very soon after the termination of Pentacrinoid life, as is seen on comparing  $r^2$ ,  $r^2$  in Plate XLI. fig. 6, and Plate XLII. fig. 7; and, as in the preceding instance, there takes place concurrently with their increase of size a gradual development of the prominences that give attachment to muscles and ligaments, with a deepening of the cavities that lie between them, as well as a progressive enlargement of the central canal.

93. Third Radials.—The change of form which the Third Radials undergo concurrently with their great increase in size, is scarcely less considerable than that of the Second; and the same tendency is manifested to lateral and vertical augmentation rather than to increase in radial length. The proximal face of the plate, which is apposed to the distal face of the second radial, rapidly increases both in width and depth; and comes like it to present an expanded surface, the ventral and dorsal margins of which form the bases of triangles formed by the ventral and dorsal faces respectively (Plate XXXVI. fig. 3, c, d). The entire sides of these triangles now form the margins of those lateral surfaces for the articulation of the first Brachials, which in the earlier period were merely a pair of facets somewhat inclined to each other on the distal extremity of the segment (Plate XLII. fig. 3,  $r^3$ ). And these lateral articular faces, as they increase in proportional dimensions, come also to present prominences and fossæ similar to those that are characteristic of the distal faces of the First Radials, which they nearly equal in size as well as resemble in appearance. The central canal, with the branches into which it

bifurcates, is progressively enlarged by the internal absorption of its wall, as in the preceding cases.

94. Oral Plates.—The removal of these first-formed plates by absorption, which we have seen to commence before the termination of Pentacrinoid life, is completed very soon after the young Antedon has entered upon its free stage of existence. The absorptive process continues to take place from above downwards; and the last traces of these plates that can be distinguished, are seen as glistening fragments of calcarcous network at the bases of five membranous valves which still fold over the tentacles forming the oral ring, in specimens which have attained a diameter of about an inch and a half. These soon disappear entirely.

95. Anal Plate.—This plate is still distinguishable in specimens that show no vestiges of the Orals; but it has undergone no increase in superficial dimensions, and is so far from being augmented in thickness that it seems rather to have been thinned by incipient absorption over its whole surface, preparatory to its complete disappearance a short time after. I do not find that either the upper part of this plate disappears before the lower (as we have seen to be the case with the Orals), or the lower before the upper; and as I have found no vestiges of it, though I have carefully sought for them, in young Antedons of about 2 inches in diameter, I conclude that the entire plate is removed at once by a continuance of absorption over its whole surface.

96. Arms.—It does not seem requisite to follow in any detail the development of the segments of the Arms; since the changes in conformation through which the first formed Brachial segments pass in their progress to maturity, are precisely analogous to those which have been already described in the Radials; and the successive production of new segments at the extremities of the arms takes place after exactly the same fashion as in the Pentacrinoid stage. The general tendency is to an increase in the diameter of the segments, which is relatively much greater than the increase in their radial length (§ 40); and with this there is an extension of their apposed articular faces, which gradually come to present the ridges and fossæ characteristic of the adult type, whilst at the syzygies these faces are brought into closer mutual approximation. The central canal by which each segment is traversed, undergoes a corresponding enlargement. The development of the Pinnæ from the basal portions of the arms, which for the most part remain destitute of them for some time after the first appearance of these lateral appendages (§ 69), takes place by the time that the Orals disappear; but these intermediate pinnæ are long in attaining the dimensions of those nearer the terminations of the arms. The increase of the Pinnæ in length, like that of the Arms themselves, partly depends upon an increase in the number of their segments, and partly on an augmentation in the length of each individual segment. How and where the new segments are added, I cannot certainly say; but it may be safely assumed that they are not developed at the terminations of the pinnules, since their peculiar terminal hook is formed when as yet the segments are few in number. And as the basal segment has a peculiar conformation for its articulation with the brachial from which the pinnule proceeds

(§ 54), I cannot think it likely that it is displaced from time to time by the interposition of a new segment between itself and the brachial. The most probable place for such interposition seems to be either between the basal and the second segment, or between the penultimate segment and the terminal claw-bearing segment. Since no such traces of incompleteness present themselves in the segments which follow the basal as would justify the former supposition, we seem compelled to adopt the latter; and it is not a little curious that the increase in the number of segments in the Stem, the Dorsal Cirrhi, the Arms, and the Pinnules should thus take place in different modes,—the new segments making their appearance in the Stem immediately beneath its highest segment (§ 63), in each Dorsal Cirrhus at its base (§ 66), in each Arm at its termination (§ 67), and in each Pinnule at the base of its terminal segment.

## EXPLANATION OF THE PLATES.

#### PLATE XXXI.

Side view of Antedon rosaceus attached by its dorsal cirrhi to a stone; drawn from a living specimen in a Vivarium.—Magnified  $3\frac{1}{2}$  diameters.

A, Disk and basal portion of the Arms of the same, as seen from above; showing the manner in which the basal pinnules arch over the ventral surface of the disk.—Magnified  $3\frac{1}{2}$  diameters.

#### PLATE XXXII.

- Fig. 1. Dorsal aspect of the Calyx of Antedon rosaceus, as seen after the removal of the dorsal cirrhi:—c, Centro-dorsal plate, entirely concealing the First Radials; r², r², Second Radials; r³, r³, Third or Axillary Radials; br¹, br¹, First Brachials.—Magnified 8 diameters.
- Fig. 2. Ventral aspect of the Calyx, as seen after the removal of the visceral mass. Around the central depression is seen a circlet of *five* pairs of Muscles, passing between the First and Second Radials; and outside these is a circlet of *ten* pairs, passing between the Third Radials and the First Brachials (see Plate XXXIV. fig. 2).—Magnified 8 diameters.
- Fig. 3. Ventral surface of the Visceral Disk, showing the mouth, m, in the centre, with five channels radiating from it, which form by their bifurcation the ten channels that pass along the Arms and give off branches to the Pinnules, the first and second of which on each arm assist in supporting the visceral mass; at  $\alpha$  is shown the Anus seated on a proboscis-like funnel that rises between two of the Radial channels.—Magnified 8 diameters.
- Fig. 4. Dorsal Cirrhi as seen radiating from the Centro-dorsal plate, c, to which they are articulated.—Magnified 15 diameters.

Fig. 5. Dorsal Cirrhi in various stages of growth and development:—a, typical mature cirrhus; b, c, d, e, f, successive stages of incomplete type; g, h, i, k, l, successive stages of complete type; m, n, cirrhi presenting most of the characters of maturity, but having less than the normal number of segments, and deficient in the opposing process.—Magnified 45 diameters.

# PLATE XXXIII.

- Fig. 1. Pentagonal Base of the Calyx of Antedon rosaceus, formed by the coalescence of the five First Radials, its dorsal surface (shown in fig. 2) having been removed, so as to lay open the radiating Axial Canals, a, a, and their communicating branches, b, b; around the central space is an irregular calcareous network, formed by the inosculation of processes sent off from the internal faces of the First Radials.—Magnified 25 diameters.
- Fig. 2. Pentagonal Base of the Calyx, formed by the coalescence of the five First Radials, with the Rosette *in situ*, as seen from its dorsal aspect, the Centro-dorsal plate having been removed.—Magnified 25 diameters.
- Fig. 3. Pentagonal Base of the Calyx, formed by the coalescence of the First Radials, as seen from its ventral aspect:—the central aperture for the passage of a prolongation of the Crinoidal Axis is surrounded by irregular processes from the inner margins of the First Radials, which connect themselves with the central portion of the Rosette; the oblique sides of the pentagon form the surfaces of articulation for the Second Radials.—Magnified 25 diameters.
- Fig. 4. Centro-dorsal plate, seen from its dorsal side after the removal of the cirrhi; showing its flattened central portion surrounded by between two and three circlets of articular sockets.—Magnified 15 diameters.
- Fig. 5. Lateral view of the same, showing the alternating arrangement of the sockets.

  —Magnified 15 diameters.
- Fig. 6. Centro-dorsal plate, seen from its ventral side after its detachment from the Pentagonal Base, showing its basin-like cavity, the bottom of which is perforated by minute apertures for the passage of the axial cords of the cirrhi; on the inturned lip of the basin are five shallow depressions, α, α, corresponding to the spout-like processes of the Rosette.—Magnified 15 diameters.
- Fig. 7. Portions of Base of Calyx at origin of Rays, in the variety showing Intervadial Plates:—c, Centro-dorsal;  $r^2$ ,  $r^2$ , Second Radials;  $r^3$ ,  $r^3$ , Third Radials: at A these intervadials are numerous, minute, and dissociated, and are obviously perisomatic in their character; at B they are fewer, larger, and more compactly arranged.—Magnified 30 diameters.
- Fig. 8. Segments of Dorsal Cirrhi; a, basal, b, from middle of length; showing the central passage surrounded by a prominent annulus, with depressions on either side for the attachment of ligaments.—Magnified 70 diameters.

- Fig. 9. Central portion of fig. 2 more enlarged, showing the Rosette in situ:—a, a, lines of junction of the First Radials; b, b, apertures formed by the coalescence of the spout-like processes of the Rosette with the inner margins of the First Radials.—Magnified 70 diameters.
- Fig. 10. Rosette separated and seen on its dorsal aspect, showing its five flattened triangular processes, a, a, and its five intermediate spout-like processes, b, b.—

  Magnified 100 diameters.
- Fig. 11. Rosette seen from the ventral side, showing around its central orifice irregular projections which coalesce with the processes given-off from the inner margins of the First Radials; a, a, triangular processes; b, b, spout-like processes.—

  Magnified 100 diameters.

## PLATE XXXIV.

The following References are common to both Figures:—

r¹, r¹, First Radials.
r², r², Second Radials.
r³, r³, Third or Axillary Radials.
br¹, br¹, First Brachials.
br², br², Second Brachials.
br³, br³, Third Brachials.

p, p, Pinnules.

- Fig. 1. Horizontal section of Calyx and basal portions of Arms of Antedon rosaceus, flattened out; showing the axial canals, a, a, of the Rays which communicate by circular branches at b, b (as in Plate XXXIII. fig. 1), and bifurcate at c, c, to pass into the Arms.—Magnified 18 diameters.
- Fig. 2. Interior of the Calyx with basal portions of Arms, of a young Antedon, to show the disposition of the Muscles:— $m^1$ ,  $m^1$ , five pairs of muscles passing between the First and Second Radials;  $m^2$ ,  $m^2$ , ten pairs of muscles passing between the Third or Axillary Radials and the First Brachials;  $m^3$ ,  $m^3$ , ten pairs of muscles passing between the Second and the Third Brachials.—Magnified 30 diameters.

#### PLATE XXXV.

- Fig. 1. Vertical Section of the Centro-dorsal Piece; consisting of the Centro-dorsal plate which forms the dome of the cavity, and which is anchylosed at the lines a, a, a to the First Radials; b, b, canals leading to the articular sockets of the cirrhi; c, basal segment of a cirrhus; d, d, axial canals of First Radials; e, e, portions of Second Radials; f, Rosette.—Magnified 70 diameters.
- Fig. 2. Longitudinal Section of three of the basal segments of a Dorsal Cirrhus, showing the central articular processes, and the ligaments interposed between their peripheral surfaces.—Magnified 70 diameters.

- Fig. 3. Longitudinal section of the terminal portion of a Dorsal Cirrhus; showing the claw articulated by the plane surface cut through at a, a, to the penultimate segment, and the movable articulation b, b, in which the fossæ for the lodgment of the ligament are much larger and deeper on the aboral side; at c, c is shown the central canal, which is continued into the cavity of the claw.—

  Magnified 70 diameters.
- Fig. 4. Section of Centro-dorsal plate taken in a plane parallel to its flattened surface; showing at b, b the canals leading to the articular sockets.—Magnified 70 diameters.

## PLATE XXXVI.

In this Plate are shown the First, Second, and Third Radials, and the First, Second, Third, Fourth, and Fifth Brachials, of Antedon rosaceus; their different aspects being designated (except in fig. 1) as follows:—

- A, internal or proximal face.
- B, external or distal face.
- c, ventral or superior face.
- D, dorsal or inferior face.
- E, lateral face.

The following References are common to the entire series:-

- a, a, Articular Ridges.
- b, b, Fossæ for Interarticular Ligaments.
- c, c, Muscular Fossæ.
- d, d, Vertical Lamellæ.
  - e, Axial Canal.
- f, f, Fossa for Elastic Ligament.
  - p, Articular Socket of Pinnule.
  - sg, Syzygy.

The magnifying power for all the Figures is 15 diameters.

- Fig. 1. First Radial: on its internal aspect (B) are shown the apertures, e, e, of the two passages by which the Axial Canal originates, and the apertures, g, g, of the circular passage by which the axial canal of each Ray communicates with the canal of the Ray on either side; h, furrow between the prominent margins of the apertures e, e; i, i, smooth inclined faces, closely adherent to those of the First Radials on either side: Λ, external face.
- Fig. 2. Second Radial.
- Fig. 3. Third or Axillary Radial; d', vertical ridge dividing the two articular faces.
- Fig. 4. First Brachial.
- Fig. 5. Second Brachial.
- Fig. 6. Third Brachial, united in c, D, and E with the Fourth.
- Fig. 7. Fourth Brachial.
- Fig. S. Fifth Brachial.

#### PLATE XXXVII.

- Fig. 1. Portion of Skeleton of Arm of Antedon rosaceus about the middle of its length, seen from its dorsal aspect; the segments of the Arms and Pinnæ remaining united by their ligaments; sg, sg, syzygies.—Magnified 15 diameters.
- Fig. 2. A similar portion somewhat nearer the base, seen from its ventral aspect, showing the Muscular fossæ and the situation of the articulations of the Pinnules.—Magnified 10 diameters.
- Fig. 3. Basal portion of the skeleton of the Arms with their Pinnules, seen from their dorsal aspect:— $r^3$ , Third Radial; 1–16, Brachial segments; sg, syzygies.—Magnified 10 diameters.
- Fig. 4. A similar portion of the Skeleton of the Arms with the Pinnules removed, seen from their ventral aspect; showing the Interarticular Ligaments, the deep Muscular fossæ lying between the vertical ridges, the syzygies, sg, and the articular sockets of the Pinnules, p, p.—Magnified 15 diameters.

#### PLATE XXXVIII.

- Fig. 1. Terminal portion of growing Arm; from a preparation in which the soft parts have been made transparent by soda, and the calcareous reticulation is shown by black-ground illumination.—Magnified 120 diameters.
- Fig. 2. Portions of Arm near its termination, showing the nearly cylindrical form of its segments:—c, c, Muscular Fossæ; p, p, Articular sockets of Pinnules; sg, syzygies.—Magnified 15 diameters.
- Fig. 3. Terminal portion of Pinnule, showing the hooks at its extremity, and the series of short segments below the last two.—Magnified 70 diameters.
- Fig. 4. Terminal portion of Skeleton of Arm, with its Pinnules, seen from its dorsal aspect.—Magnified 15 diameters.
- Fig. 5. Segment of Arm from about the middle of its length; A, distal face; B, proximal face; c, side view.—Magnified 15 diameters.
  - [N.B. Figures A and B have been drawn in an inverted position with reference to those in Plate XXXVI.; the *upper* margin being here the *dorsal*, and the *lower* the *ventral*].
- Fig. 6. Portion of an Arm that has been broken at the first syzygy, with new arm sprouting from this.—Magnified 10 diameters.
- Fig. 7. Single Arm growing from the Second Radial,  $r^2$ , the Third Radial being altogether deficient. The segments of this arm have their normal size and proportions; and the syzygies occur at their regular intervals.—Magnified 10 diameters.
- Fig. 8. Calyx and basal portion of Arms of a specimen which seems at A to have lost one of its Rays at the junction of the First and Second Radials, a wew Ray and Arms having been produced on a smaller scale; whilst at B the Second

Brachial of one of the Arms acts as an axillary segment, bearing two small Arms.—Magnified 3½ diameters.

- Fig. 9. Calyx and Basal portion of Arms of a specimen which seems, like the last, to have lost one of its Rays at the junction of the First and Second Radials, the Ray and Arms having been reproduced on a smaller scale.—Magnified 3½ diameters.
- Fig. 10. Basal portion of Arms with the soft parts removed from their ventral surface, so as to show the disposition of the Muscles;  $r^3$ , Third Radial, with its pair of Muscles on either side connecting it with  $br^1$  the First Brachial; between this and the Second Brachial,  $br^2$ , there is only ligamentous union; the next pair of muscles connects the Second with the Third Brachial,  $br^3$ ; between the Third and the Fourth Brachial there is a syzygy, sg; and beyond this the muscles connect every segment with that which succeeds it, except where a syzygy intervenes. The small muscles connecting the segments of the Pinnules are also shown.—Magnified 15 diameters.
- Fig. 11. Vertical Longitudinal Section of an Arm taken near its base, to show the arrangement of its Muscles, m, m, and its Ligaments, l, l, and the interruption of these at the syzygy, sg.—Magnified 15 diameters. (See also Plate XLIII. fig. 6.)

## PLATE XXXIX.

- Fig. 1. Group of Pentacrinoid larvæ of Antedon rosaceus in different stages:—A, showing the Basals, b, b, the circlet of First Radials,  $r^i$ ,  $r^i$ , already complete, the rudimentary Second and Third Radials supported by this, and the circlet of Orals, o, o, alternating with these and resting on the First Radials; B, showing the incipient development of the Arms from the extremities of the Third Radials, the relative positions of the other parts being but little changed, and the Dorsal Cirrhi not having yet made their appearance (see Plate XLI. fig. 1 for a representation of the skeleton in this stage on a larger scale); c, showing the further development of the Arms, the incipient opening-out of the Calyx occasioned by the increased development of the First Radials, and the first appearance of the Dorsal Cirrhi; D, showing the first appearance of Pinnules at the extremities of the Arms, the further opening-out of the Calyx (bringing the vent into view), and the formation of the first whorl of Dorsal Cirrhi (see Plate XL.); E, showing the Pentacrinoid ready to assume its free condition, two rows of Dorsal Cirrhi being now completed, the Arms being considerably elongated by the addition of new segments, and several pairs of Pinnules being formed at their extremities.—Magnified 15 diameters.
- Fig. 2. Skeleton of early Pentacrinoid larva, from a dried specimen, showing the mode in which the Calyx can be (in that stage) completely closed in by the folding together of the Orals, o, o.—Magnified 70 diameters.

Fig. 3. Skeleton of the Pentacrinoid larva represented in Fig. 1, c, showing two rudimentary segments of the Stem, the incipient development of the Dorsal Cirrhi, the Basals, b, b, the First, Second, and Third Radials,  $r^1, r^1$ ,  $r^2, r^2$ ,  $r^3, r^3$ , and the Anal, a, now being lifted up from between the First Radials.—Magnified 50 diameters.

#### PLATE XL.

- Fig. 1. More enlarged view of a Pentacrinoid larva of Antedon rosaceus, in a stage nearly corresponding with that shown in Plate XXXIX. fig. 1, D, the nearest Ray having been removed so as to bring into view the Oral apparatus:—cd, Centro-dorsal plate, bearing two cirrhi, cir, cir, one rudimentary, another in an advanced stage of development;  $r^1, r^1, r^2, r^2, r^3, r^3$ , First, Second, and Third Radials; o, o, Orals, now completely separated from the Radials by the intervention of the membranous Perisome.—Magnified 60 diameters.
- Fig. 2. Calyx of the same specimen seen from the other side, showing the Centro-dorsal plate, cd, bearing two cirrhi, cir, cir, one rudimentary, the other still retaining its rudimentary form, the First, Second, and Third Radials, r¹, r¹, r², r², r³, r³, and the Anal, α, now lifted out from between the First Radials by the development of the prominent Vent, v, to which it is attached.—Magnified 60 diameters.

#### PLATE XLI.

- Fig. 1. Skeleton of Pentacrinoid at the time of the first development of the Arms, and before the first appearance of the dorsal cirrhi:—b, b, Basals; r¹, r¹, First Radials; α, Anal; r², r², Second Radials; ο, ο, Orals; r³, r³, Third Radials.— Magnified 100 diameters.
- Fig. 2. Separated portions of the skeleton of the Calyx of a Pentacrinoid at the epoch of its detachment from the stem:—B, external and internal (dorsal and ventral) faces of Basals; R¹, external and internal faces of First Radials; R², external and internal faces of Second Radials; R³, external and internal faces of Third Radials; A, Anal; c, ventral aspect of Centro-dorsal basin.—Magnified 100 diameters.
- Fig. 3. Basals in process of conversion into Rosette:—a, dorsal aspect, showing partial absorption of first-formed lamella; b, another specimen turned a little to one side, showing the more complete absorption of the original lamella; c, d, ventral and dorsal aspects of a basal which has been nearly modelled by absorption and outgrowth into the form requisite to constitute the Rosette (Plate XXXIII. figs. 10, 11) by union with its fellows.—Magnified 100 diameters.
- Fig. 4. Portion of the dried Stem of a young Pentacrinoid; showing the prominent annulus in the middle of each segment.—Magnified 70 diameters.

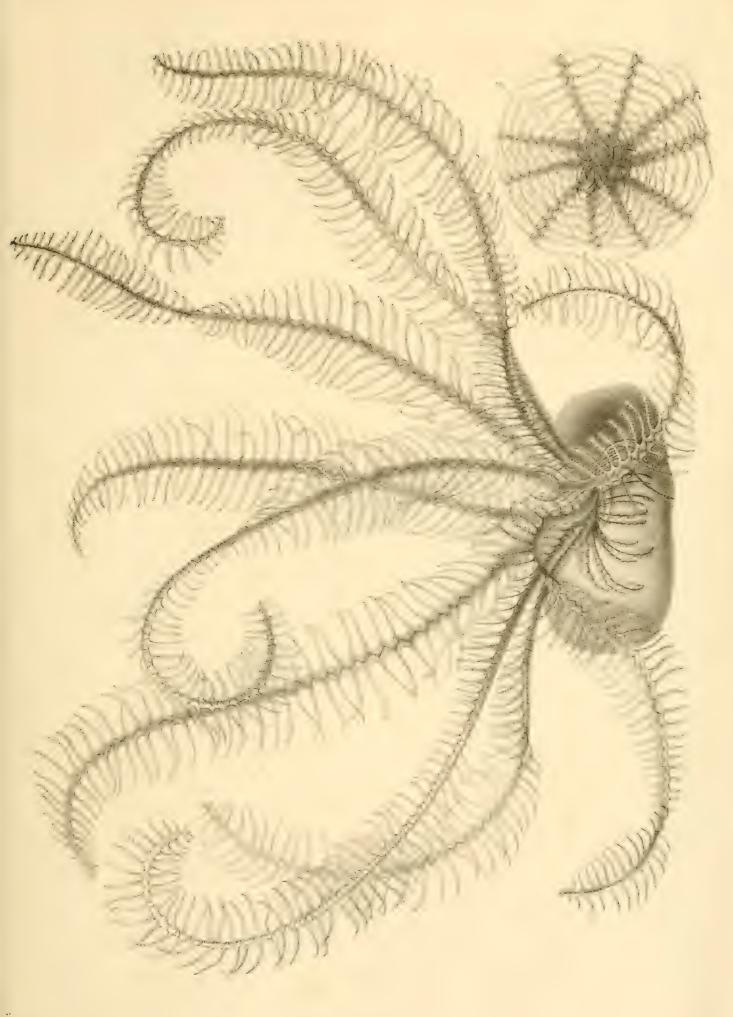
- Fig. 5. Skeleton of the Calyx of a Pentacrinoid nearly ripe for detachment, as seen from its internal or ventral aspect, the centro-dorsal plate having been removed;
  b, b, Basals; r¹, r¹, First Radials.—Magnified 50 diameters.
- Fig. 6. The same, as seen from its external or dorsal aspect:—c, central pore for the passage of the sarcodic axis through the Centro-dorsal plate; b, b, Basals; r¹, r¹, First Radials; r², r², Second Radials; r³, r³, Third or Axillary Radials; br¹, br¹, Brachials; a, Anal.—Magnified 50 diameters.

# PLATE XLII.

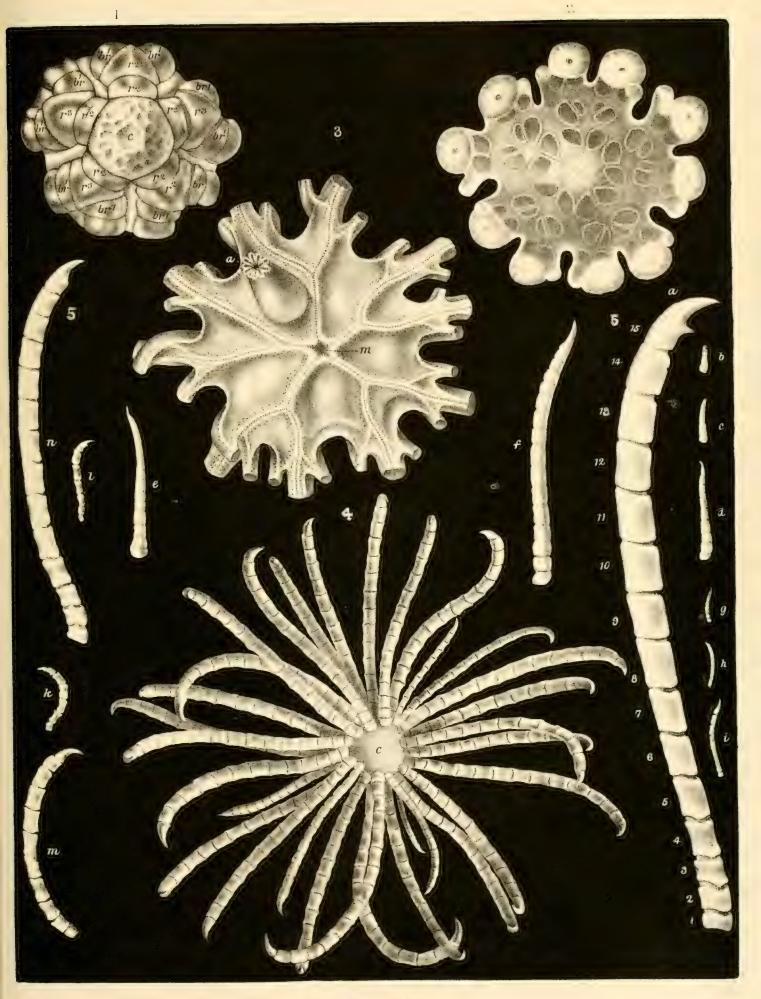
- Fig. 1. Incipient Rosette (see Plate XXXIII. figs. 10, 11) formed by the coalescence of the five altered Basals, in a young *Antedon*.—Magnified 120 diameters.
- Fig. 2. Skeleton of Base of Calyx of young Antedon, seen from its internal or ventral side; showing the five basals (b) altered by endogenous growth, in preparation for the formation of the Rosette.—Magnified 100 diameters.
- Fig. 3. Calyx of young Antedon just detached, seen from its dorsal side, showing five Cirrhi of the mature type and five of the rudimentary type, the Radial and Brachial plates, and the extension of the visceral disk as far as the Third Radial.—Magnified 25 diameters.
- Fig. 4. Skeleton of the terminal portion of the Arms of a mature Pentacrinoid:—A, ventral aspect; B, dorsal aspect.—Magnified 100 diameters.
- Fig. 5. Skeleton of the basal portions of the Arms of a mature Pentacrinoid:—A, ventral aspect; B, dorsal aspect.—Magnified 100 diameters.
- Fig. 6. Skeleton of base of Calyx of young Antedon, seen from its ventral aspect; showing the five Basals grouped around b, and traversed by canals for the radiating cords of the sarcodic axis, of which a trunk enters each basal from the central space, and then subdivides into two branches, that pass into the two Radials between which the salient angle of the basal projects; thus each First Radial receives cords from two basals, and these are lodged in two Canals which coalesce into one towards its distal border, each of them having first become connected by a lateral branch with the like canal in its contiguous First Radial.—Magnified 70 diameters.
- Fig. 7. The same viewed from its dorsal aspect, the Centro-dorsal plate having been removed; showing that the central space around b on the under side has been enlarged by the absorption of part of the original Basals, though it is still contracted, nearer the cavity of the Calyx, by the secondary endogenous growth: the system of Axial Canals is displayed as in the preceding figure.—Magnified 70 diameters.

## PLATE XLIII.

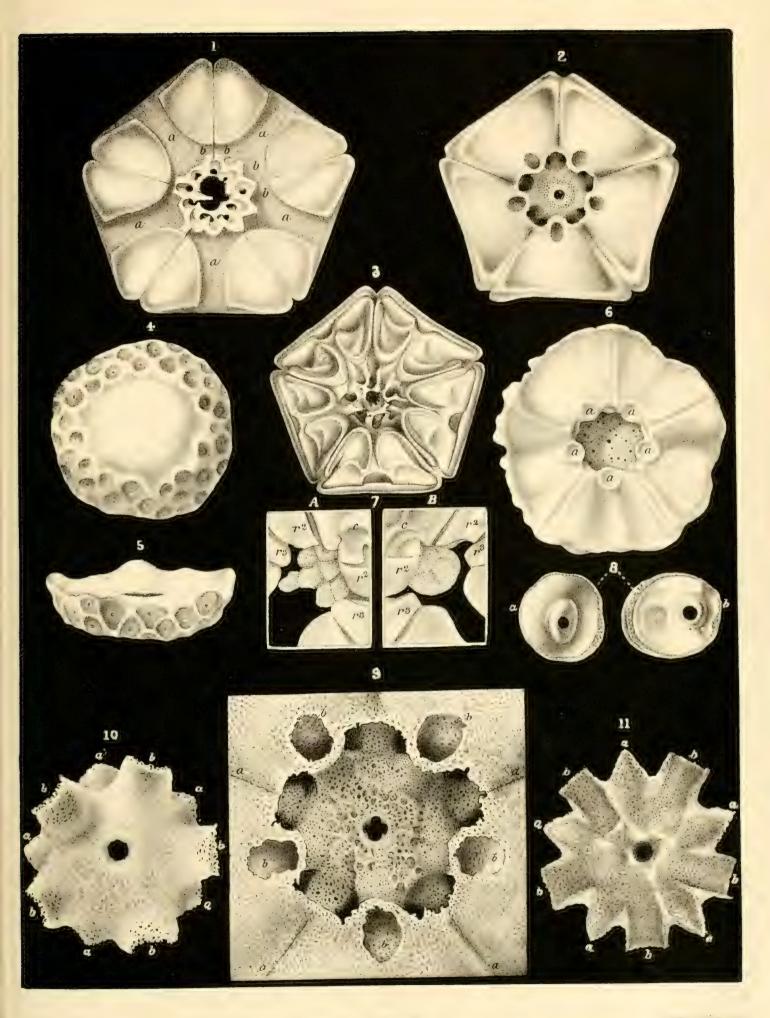
- Fig. 1. Portion of the Sarcodic Basis of the Skeleton of Antedon rosaceus, showing the granular glomeruli which occupy the interspaces of the calcareous reticulation.—Magnified 120 diameters.
- Fig. 2. Transverse section of a decalcified Arm at a syzygy, showing the radiating extensions of sarcodic substance which occupy the grooves of the apposed calcareous segments.—Magnified 30 diameters.
- Fig. 3. Ligamentous substance uniting the dorsal portions of the Brachial segments, magnified 70 diameters; 3A, portion of the same magnified 250 diameters.
- Fig. 4. Muscular fibres, magnified 250 diameters, showing at a their enlarged terminations; Λ, separated fibres enlarged 870 diameters, showing nuclear (!) corpuscles, a, b, c.
- Fig. 4. Vertical section of the decalcified skeleton of the basal portion of an Arm of Antedon rosaceus, showing the disposition of the Muscles and Ligaments:—
  s, s, s, bodies of the segments perforated by the Axial Canal, a, a, and connected by the Interarticular Ligaments, l<sup>1</sup>, l<sup>1</sup>, and the Elastic Ligaments, l<sup>2</sup>, l<sup>2</sup>;
  s<sup>1</sup>, s<sup>1</sup>, vertical lamellæ, the spaces between which are occupied by the Muscles m, m.—Magnified 55 diameters.
- Fig. 4. Horizontal section of the decalcified skeleton of the basal portion of an Arm, passing through the Axial Canal a, a, and showing the alternating obliquity of the articulations, as shown in the disposition of the ligaments  $l^2$ ,  $l^2$ ; at sg, sg, are shown in transverse section the radiating extensions of sarcodic substance interposed between the syzygies, shown in fig. 2.—Magnified 35 diameters.







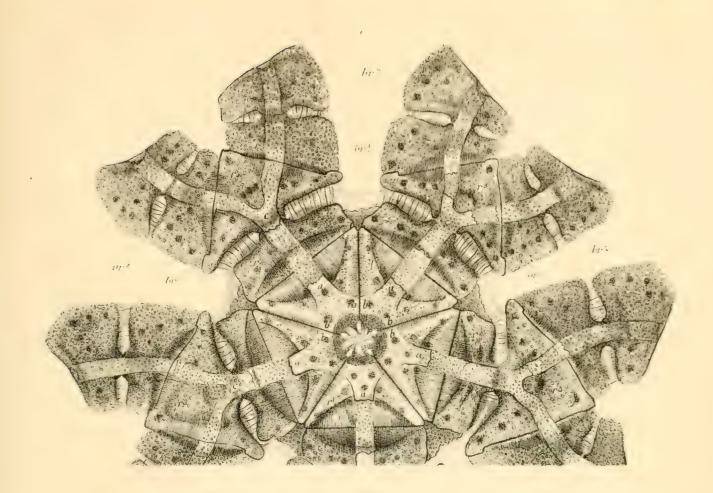


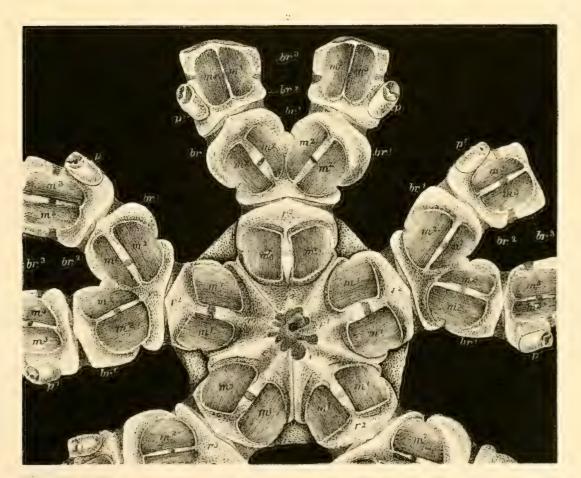


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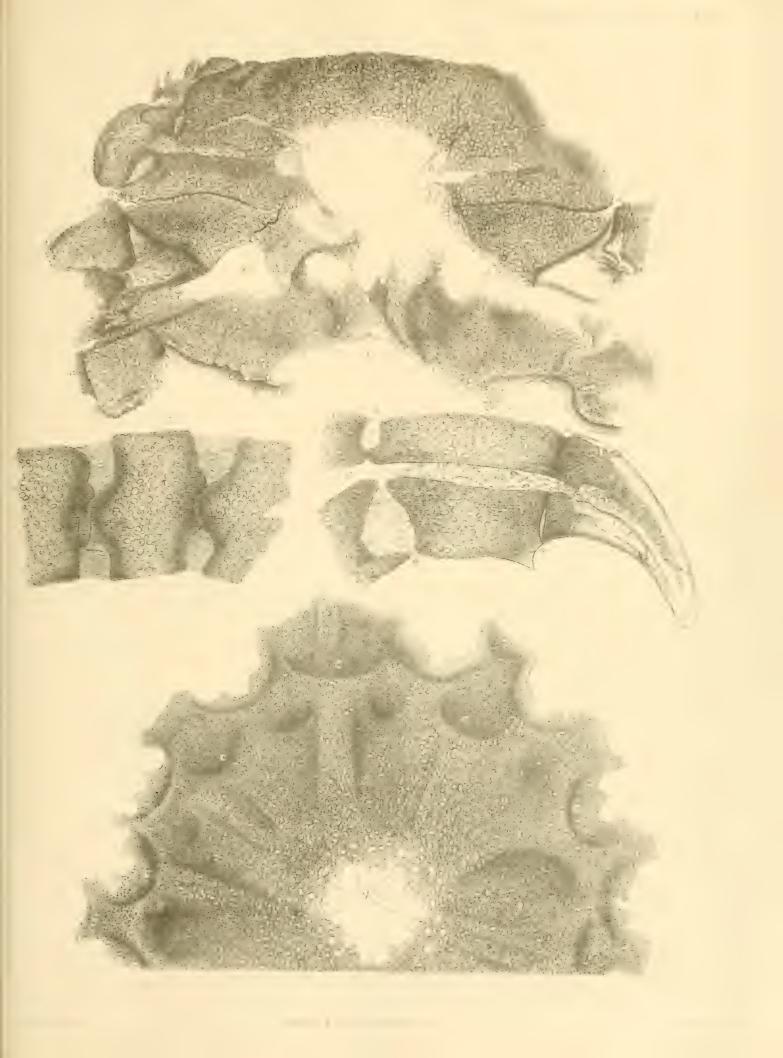
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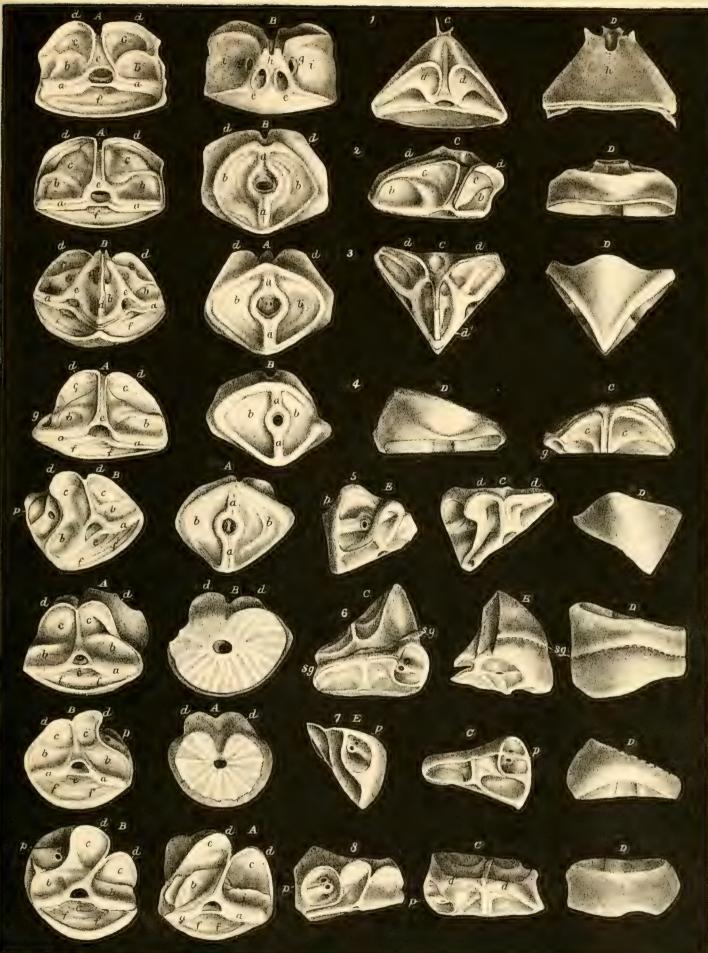




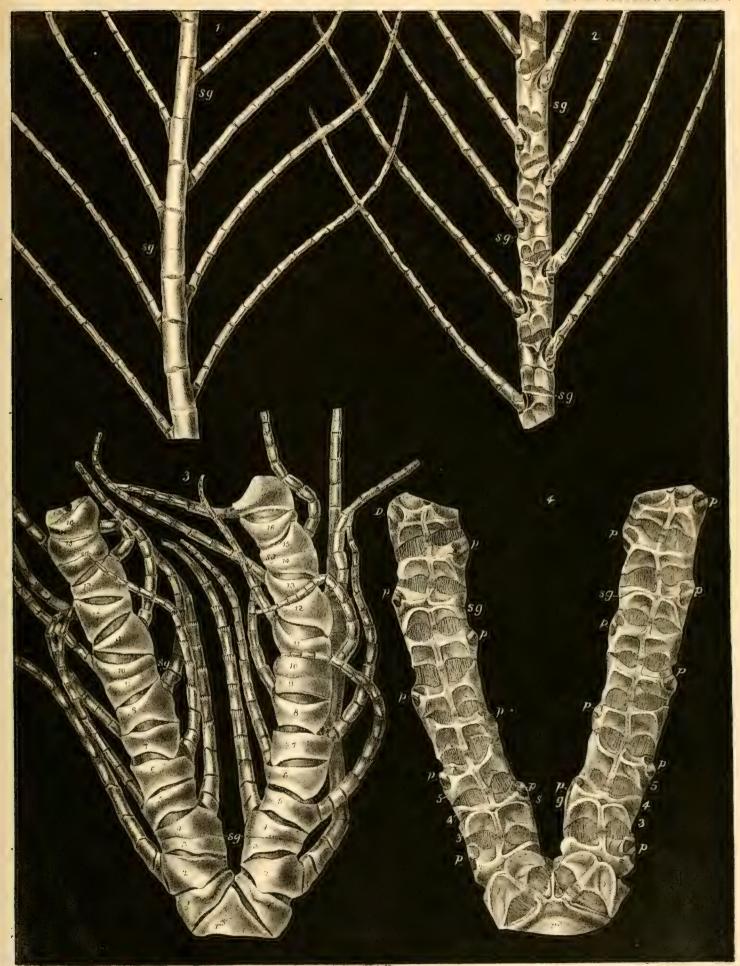




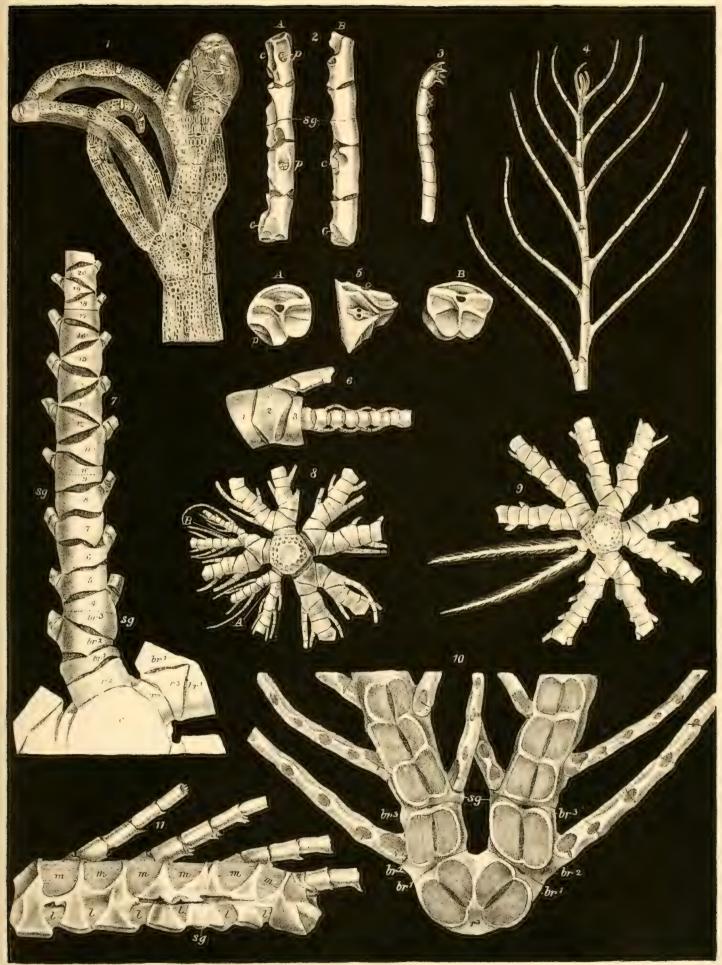






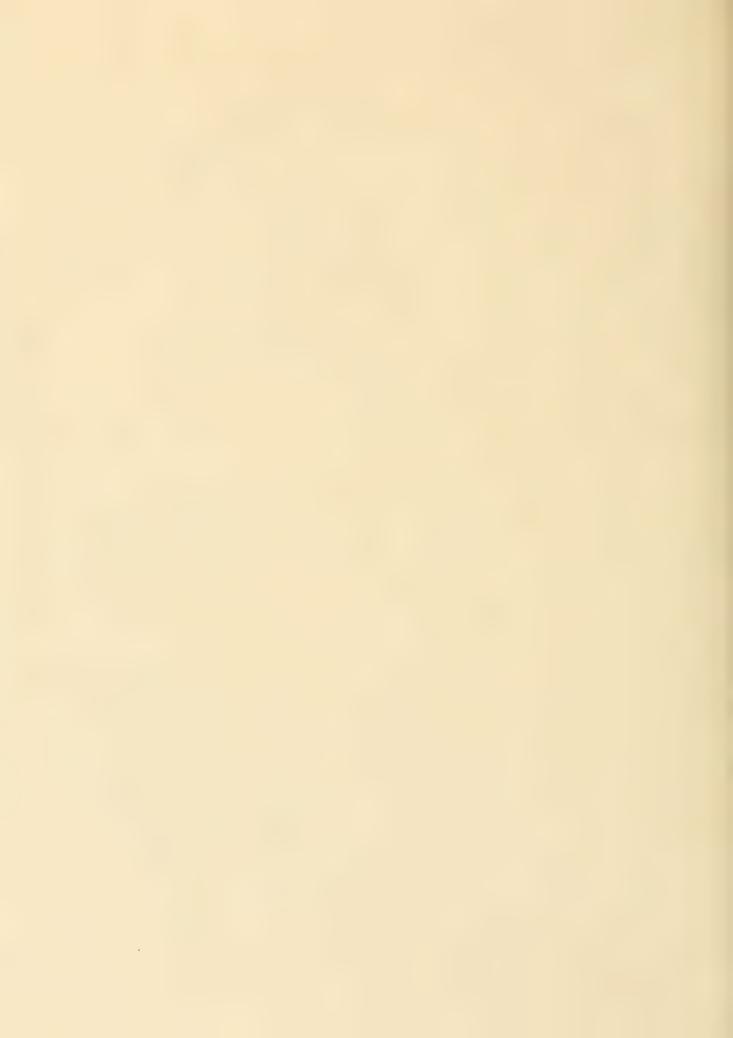


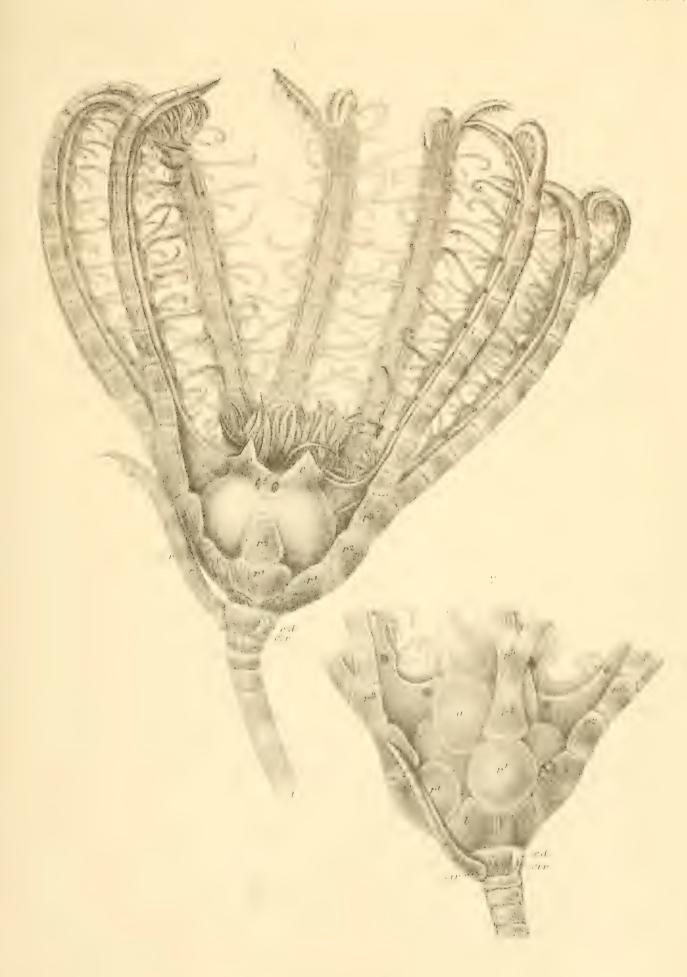




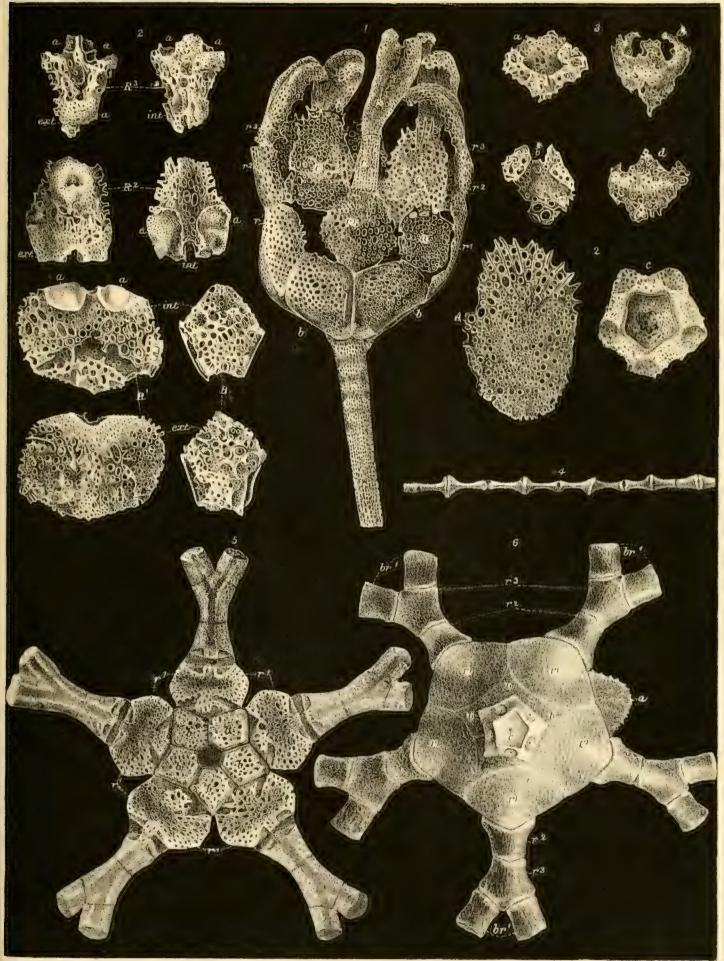






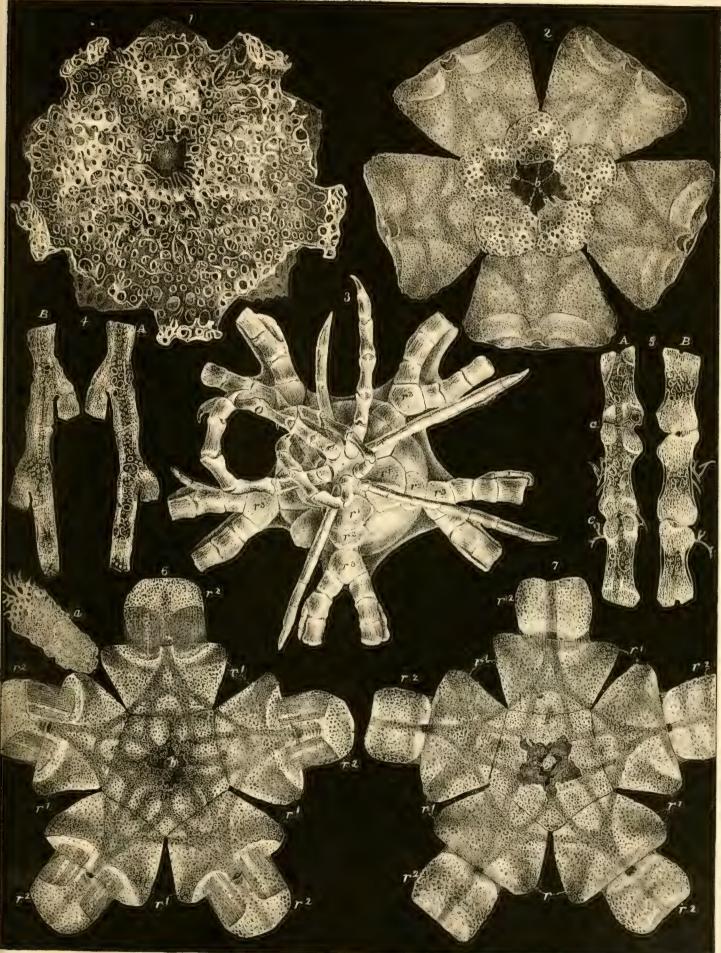




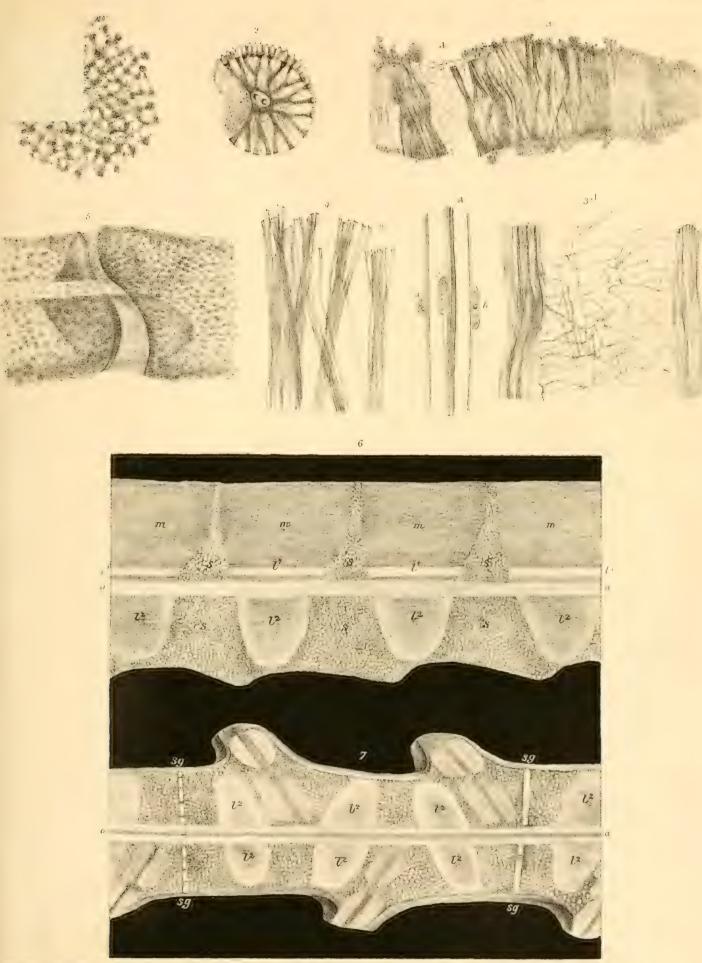


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